VOLUME XLVIII NUMBER 6

# BOTANICAL GAZETTE

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## DIOON SPINULOSUM[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 131

CHARLES J. CHAMBERLAIN

(WITH SEVEN FIGURES)

Three well-defined species of Dioon have been found in the Mexican tropics: *D. edule* Lindl., *D. spinulosum* Dyer, and *D. Purpusii* Rose. *D. edule*, which was described as early as 1843, is now quite well known. Although *D. Purpusii* was described only a few months ago, the species had often been seen, but had been mistaken for *D. edule*, which it resembles in its general appearance. I was told by a Mexican botanist that I should find *D. edule* along the Mexican Southern R. R. in the neighborhood of Santa Catarina, State of Oaxaca. He said there was no other cycad in that region. The plant was easily found, and I at once saw that it was a new species intermediate between *D. spinulosum* and *D. edule*. The plant called *D. edule* in *fig. 101* of WIELAND'S *American fossil cycads* is the new *D. Purpusii*, as plainly indicated by the staminate cone and by the leaves. MACDOUGAL and ROSE collected cones of the new species in 1906 in the Tomellin cañon, where it was well shaded by bushes and small trees. PURPUS in 1908 collected seeds and bracts in the Sierra Mixteca, Puebla. In April of the same year I saw the species at various places between Santa Catarina and Tomellin, growing in dry, exposed situations, associated with cacti and Beaucarnea. ROSE[2] describes the staminate sporophylls as "bracts with recurved ovate tips," apparently supposing that the sporangia were borne on the

Investigation prosecuted with the aid of a grant from the Botanical Society of America.

[2] ROSE, J. N., Studies of Mexican and Central American plants. Contrib. U. S. Nat. Herb. **12**:259–302. 1909.

adaxial surface, but of course they are on the under surface and the tips point up instead of down. His description of "seeds about $4^{cm}$ in diameter" needs confirmation; $4^{cm}$ in length would be more probable.

In general habit, in the straight, stiff, ascending leaves, *D. Purpusii* resembles *D. edule*, and the leaflets have the texture of those of *D. edule*, but they retain in some degree the spinulose character of those of *D. spinulosum*. In the number of sporangia on a microsporophyll, *D. Purpusii* is intermediate between *D. spinulosum* and *D. edule*. The ovulate sporophyll is rather slender and tapers gradually to a point, in this feature resembling *D. edule* and differing decidedly from *D. spinulosum*.

*Dioon spinulosum* Dyer was described by EICHLER[3] in 1883, the description being based upon a few leaves and a few trunks without leaves. Since the largest leaf was only $65^{cm}$ in length, the plants must have been very small. One of the trunks received by EICHLER produced a leaf which his figure shows to be that of a plant only a few years old. The material came from a nursery in Cordoba, State of Vera Cruz, Mexico, and, according to the gardener, the plants grew wild in the neighborhood of Tuxtla. The striking feature is the spinulose leaf. No cones were found, and so EICHLER remarks that it might seem doubtful whether the plant is really a Dioon ("Es möchte daher zweifelhaft erscheinen, ob die Pflanze wirklich ein Dioon ist").

DYER obtained a leaf from Yucatan, and since the locality was given as Progreso, the leaf probably came from a cultivated specimen. EICHLER agreed that DYER should describe the new species. The description, based upon the single leaf, is as follows:[4]

*Folia* breviter petiolata, elongato-lanceolata, rigida, plana, pinnatisecta, ad 3 pedes longa; segmentis circiter 70 utroque latere, mediis majoribus subopositis lineari-lanceolatis breviter acuminatis 18–23-nerviis, ad 4 pollices longis media latitudine semipollicaribus, basi angustiore, utroque latere spinulis pungentibus basim versus integerrimis, inferioribus in dentes palmatifidos desinentibus. *Strobili*. . . . . South Mexico, Tuxtla; Yucatan, Progreso. (C. J. Hoge). Herb. Kew.

[3] EICHLER, A. W., Ein neues Dioon. Gartenflora **2**:411–413. 1883.

[4] DYER, W. T. THISTLETON, Cycadaceae, in Biologia Centrali-Americana Botany **3**:190–195. 1882–1886.

During my second trip to Mexico, in 1906, I saw small specimens of *Dioon spinulosum* in the park at Vera Cruz, but did not find it growing wild. Gov. TEODORE A. DEHESA, of the State of Vera Cruz, who has repeatedly assisted me in my investigation of Mexican cycads, again used his influence in my behalf, and I am also under renewed obligations to Mr. ALEXANDER M. GAW, of the State Bureau of Information, Jalapa, Mexico, for his continued interest and active cooperation both in securing material and often in furnishing field notes.

Mr. GAW found that the plants in the park at Vera Cruz came from Tlacotalpam, a town southeast of Vera Cruz, and he also found that most people do not distinguish the two species, *D. edule* and *D. spinulosum*, for he was told that the plants in the park at Vera Cruz could be found growing wild in the vicinity of Tlacotalpam, Catemaco, and elsewhere in the canton of Tuxtlas, and between Palmar and Colorado on the Interoceanic R. R. Doubtless the information in regard to the first three places was correct, but since I had found only *D. edule* in the Palmar-Colorado region, Mr. GAW sent a man through that entire district with a leaf of *D. spinulosum* as a guide. The man found *D. edule* in abundance, but failed to find a single specimen of *D. spinulosum*. In Vera Cruz the plant is called *palma de Dolores*, the same name which in the Jalapa region is applied to *D. edule*. The name *tio tamal*, which is commonly given to *D. edule* because the seeds are used in making *tamales*, does not seem to be applied to *D. spinulosum*, although its seeds are edible. The natives of the coast region call both the plant and the seeds *chicalitos*, a name which I have not heard applied to *D. edule*.

From a park in Tlacotalpam Mr. GAW secured a large ovulate cone of *D. spinulosum*, and he was told that the specimen came from the Sierra de Oaxaca Mountains near Tuxtepec, where the plant was said to be very abundant. As the Tlacotalpam cone had only abortive seeds, Mr. GAW, after repeated efforts, succeeded in securing from the Tuxtepec region an ovulate cone in which pollination and fertilization had taken place. Later he secured a cone with ripe seeds, which germinated readily. With the material Mr. GAW sent the rather startling information that, according to the natives, the cones are borne below the crown of leaves and not above the crown, as in *D. edule*.

In March 1908 I visited southern Mexico to collect *D. spinulosum* While on the way to Tuxtepec, I was informed that a plant which seemed to agree with my description, except that it was much taller, could be found near Tierra Blanca. In the mountains west and a little north of Tierra Blanca I found a few specimens and was told that plants were more numerous a few miles farther south. The information was correct, for on the immense hacienda of the Joliet Tropical Plantation Company, a short distance from Tierra Blanca and about 60 miles south of Vera Cruz, magnificent specimens are abundant. Mr. J. C. DENNIS, superintendent of the plantation, very generously furnished horses, guides, and the hospitality of his palatial home while I explored the mountains and secured photographs and material. The plant is usually well shaded, growing among the prevailing limestone rocks which have given name (Tierra Blanca) to the region.

From Tuxtepec, a town on the Papaloapam River about forty miles southwest of Tierra Blanca, half a day's ride on horseback brings one to the mountains where *D. spinulosum* is as abundant as at Tierra Blanca. In some places it is the only large plant, and it would not be an exaggeration to speak of a Dioon forest. Beautiful specimens, which might have been the pride of any conservatory, had been cut down to get the cones, because it was easier to cut the tree than to climb it. The natives use the young seeds in making *tamales*, as in *D. edule*, and at a later stage the dry stony seed coat is a common plaything for children. At Tuxtepec the dry seeds, each pierced with two holes, sell for fifteen cents a dozen. The Indians said that the plant extends some distance farther south, but that it does not occur on the western (Oaxaca) side of the mountains.

*Dioon spinulosum*, with the exception of the Australian *Cycas media*, is the tallest cycad known, and its slender trunk with a large crown of leaves gives it the appearance of a palm (*fig. 1*). I measured specimens $12^m$ in height, and Drs. BARNES and LAND, visiting the Tierra Blanca region a few months after my return, found specimens more than $16^m$ in height, almost as high as the tallest known specimens of *Cycas media*. The slender trunk and graceful curve of leaves are in striking contrast with the stocky trunk and straight, rigid, ascending leaves of *D. edule*.

FIG. 1.—*Dioon spinulosum* on the Hacienda de Joliet near Tierra Blanca, March 1908; the tallest plant is about 10m in height.

The ribbed surface of the trunk is due to successive crowns, and affords some basis for an estimate of the age of the plant, but in the lower part of the trunk of tall specimens the ribs may become too obscure for accurate counting. The scars of the individual leaves, which are so distinct in *D. edule*, are so obscure in *D. spinulosum* that counting in the lower portion of large trunks is out of the question. Whether the duration of the crown is two years, as in *D. edule*, I was not able to determine, but assuming the duration to be two years, the tallest specimens might not be more than 400 years old. However, any estimate can be little more than a guess, until the duration of crowns, and the effect of scale leaves, cones, and resting periods upon the growth of the trunk have been studied much more carefully. Still, I am inclined to believe that a $10^{m}$ specimen is no older than a $1^{m}$ specimen of *D. edule*.

At the base the trunk is much enlarged, often having twice as great a diameter as it has $0.5^{m}$ higher up. The roots are often exposed for considerable distances, especially in precipitous places, where a root may hang down along the surface of the rock. One root hanging down in this way was exposed for a distance of more than $12^{m}$ and was $5^{cm}$ in diameter where it again entered the soil.

Cutting through the trunk, which is not nearly so hard as that of *D. edule*, it is seen that there is a single zone of wood surrounding the large pith. The origin and development of the vascular cylinder, as seen in embryos and young seedlings, is being studied by HELEN A. DORETY.

Both EICHLER and DYER gave accurate descriptions of the leaves as they appear on small plants. EICHLER's largest leaf ($65^{cm}$ in length) had 38 pinnae, the lowest of which were rudimentary. DYER's leaf was about $1^{m}$ long, with 70 pinnae on each side. On plants $2^{m}$ or more in height the leaves reach their full size, so that leaves $2^{m}$ long, with 100 leaflets on each side, are not uncommon, while one leaf measured $2.2^{m}$ in length and had 117 leaflets on each side, the leaflets being $20^{cm}$ long and $10^{mm}$ wide. There is great variation in the leaflets, some only $14$–$15^{cm}$ long being $15^{mm}$ wide. There are 5–8 sharp spines on each margin of the leaflets of large leaves. The lower leaflets become more and more reduced, until the lowest ones are nothing but spines, so that the leaf bears considerable resemblance

to that of Encephalartos. The leaves of seedlings have comparatively few leaflets, the first leaf sometimes having less than a dozen on each side. It is interesting to note that in seedlings the leaves have no reduced leaflets, even the lowest being as perfectly formed as those in the middle of the leaf. The leaflets of seedlings have fewer spines than those of older plants, there being only 2–6 on each margin. The midrib is not so large as in *D. edule* and the leaves are much thinner. A few leaflets of a leaf of medium size are shown in *fig. 2*.

Remembering that the natives had reported cones growing below the crowns, one would naturally think of the condition in Bennettitales.

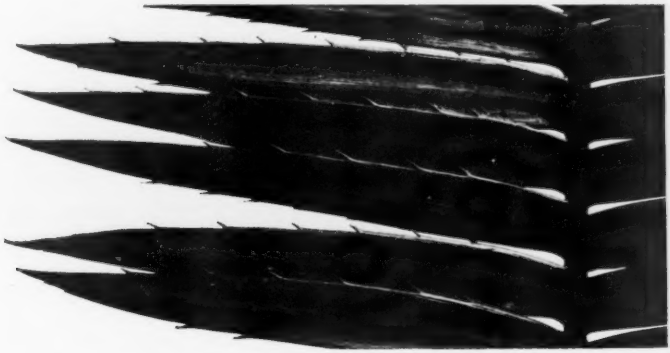


FIG. 2.—Portion of leaf of *Dioon spinulosum* from a specimen at Tlacotalpam; $\times\frac{3}{4}$; the cone shown in *fig. 4* came from the same plant.

A glance at *fig. 3* will show that the cone does hang down below the crown. An examination of the apex of the stem shows, however, that the cone is borne in the center of the crown as in *D. edule*, but that a considerable elongation of the peduncle, together with the great weight of the cone, causes the cone to bend over, slip between the leaves, and thus hang below the crown. Consequently no seeds are found in the nest of the crown as is so commonly the case in *D. edule*, where the germination of seeds in this position often gives rise to the appearance of branching. In *D. spinulosum* branching is rare. Seedlings are found for a considerable distance around the large ovulate plants. The natives say that at maturity the cone bursts with a loud noise, scattering the seeds, or *coyoles*, the plant being called *coyolillo*.

FIG. 3.—*Dioon spinulosum* with ovulate cone, on the Hacienda de Joliet, March 1908.

The ovulate cone is the largest yet known for any gymnosperm. In March, cones weighing 14 kilos were not infrequent, and occasionally a cone had reached a weight of 15 kilos. Since the seeds are not fully mature until October, it is safe to assume that the cones increase somewhat in weight after March, the time of my visit. The cone is cylindrical ovoid (*fig. 4*), its general habit distinguishing it at once from the ovoid cone of *D. edule*. It reaches a length of 50$^{cm}$ and a diameter of 27$^{cm}$, but the average cone is about 20 per cent. smaller than these measurements.

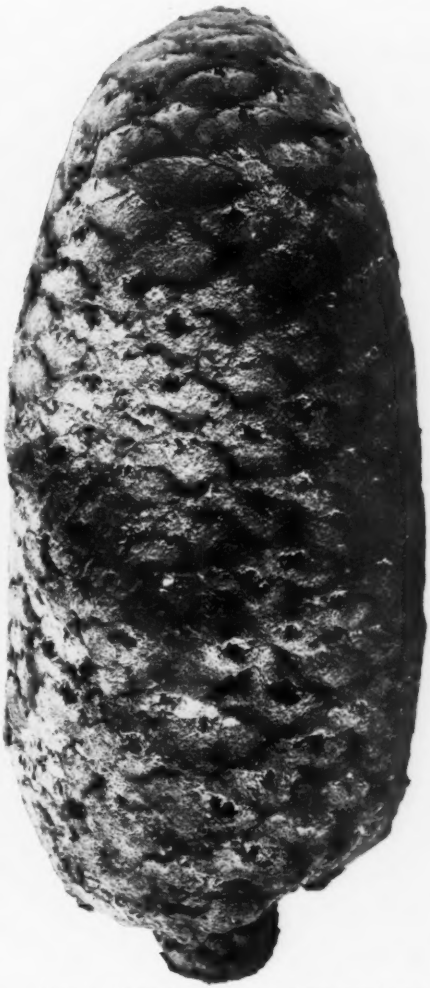


FIG. 4.—*Dioon spinulosum;* ovulate cone from a cultivated plant at Tlacotalpam; ×⅓; November 1906.

The ovulate sporophylls are very hairy, as in *D. edule* and *D. Purpusii*, but are much more closely imbricated, there being no projecting tips as is always the case in the upper part of the cone of *D. edule* and probably in *D. Purpusii*. In regard to the latter species, however, my statement is based upon only a single sporophyll. The

sporophyll of *D. spinulosum* is thick, fleshy, and rounded or obtuse at the apex, contrasting again with the long tapering sporophylls of *D. edule* and *D. Purpusii*. The contour of the exposed portion of the sporophylls and the close imbrication is seen in *fig. 4*, especially near the apex of the cone.

The seeds are white and perfectly smooth, but may become slightly yellowish when mature; their length varies from 4 to $5.5^{cm}$ and the diameter from 2.5 to $3.5^{cm}$. Some of the ovules have the

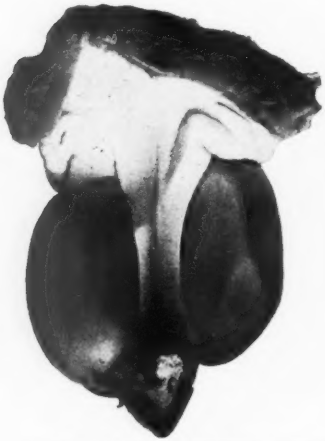


FIG. 5.—*Dioon spinulosum;* dorsal view of an ordinary sporophyll, the ovule on the left showing the false stalk; from a cone received from Tuxtepec, April 1907. ×¾.

FIG. 6.—*Dioon spinulosum;* ovulate sporophyll, from the cone shown in *fig. 4*, with five ovules, three of which can be seen on the left side, but only a portion of one of the two on the right side is visible. ×¾.

false stalk, characteristic of the genus, but it is not as frequent as in *D. edule* (*fig. 5*). In one cone, with only abortive ovules, there were frequently more than two ovules on a sporophyll, in some cases as many as five or six (*fig. 6*). Cycas, the most ancient genus of the family, regularly produces more than two ovules on a sporophyll, and in Dioon the production of more than two ovules is doubtless a recurrence of the ancient habit. In rare cases, I have noted as many as four ovules on the sporophylls of *Zamia floridana* and *Ceratozamia mexicana*.

As yet I have obtained only one staminate cone, and that not from the field but from Professor TRELEASE, of the Missouri Botanical Garden. Where the specimen came from could not be determined, except that it had been secured from the nursery of W. A. MANDA (S. Orange, N. J.), who had gotten it in a miscellaneous collection of unknown sources. This cone, which arrived in Chicago July 25, 1907, measured 21$^{cm}$ in length by 10$^{cm}$ in diameter, and since the pollen was nearly mature, this must be about the size before the elongation of the axis begins to separate the sporophylls and liberate the pollen. The general appearance of the cone is shown in *fig.* 7.

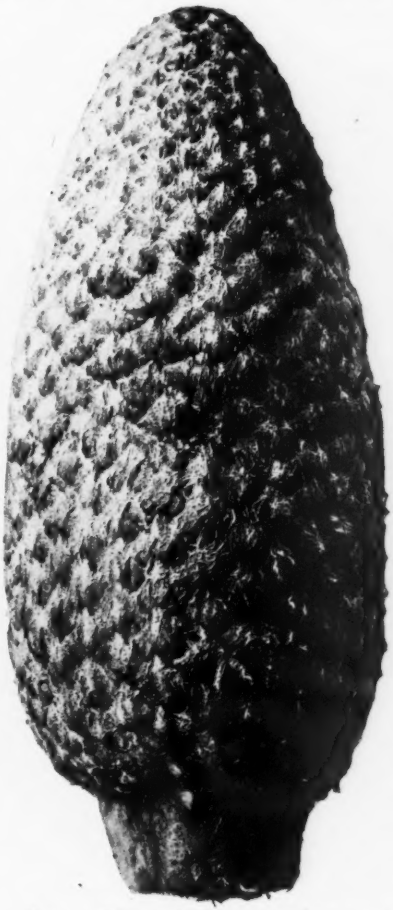


FIG. 7.—*Dioon spinulosum;* staminate cone from a plant in the Missouri Botanical Garden, July 1907. ×⅔.

The shape of the microsporophyll and its general appearance is about as in *D. edule,* except that the microsporangia are much more numerous, the average number on a microsporophyll being about 750; while in *D. edule* the average falls a little below 300. The number in *D. Purpusii* is between 300 and 400. In all three species the sporangia are in sori of 3, 4, 5, and 6 sporangia, with 4 and 5 the most frequent numbers.

While it is hardly safe to arrange the three species in an evolutionary sequence before the life histories have been studied, it seems to me that *D. spinulosum* is the oldest and *D. edule* the most recent, so that the series should be *D. spinulosum*, *D. Purpusii*, and *D. edule*. In favor of this sequence it may be said that *D. spinulosum* has a spinulose leaf throughout its life history, while *D. edule* shows the spinulose character only in the seedling, the later leaves gradually becoming entire. *D. Purpusii* has a leaf which is slightly but constantly spinulose in the adult plant. Its seedling is not known. Regarding the spinulose character of the seedling leaf of *D. edule* as due to recapitulation, *D. edule* is a later development than *D. spinulosum* and has come either from *D. spinulosum* or from some unknown form with spinulose leaves. The leaves of *D. edule* and *D. Purpusii* present about such characters as we should expect in *D. spinulosum*, if this species should be brought from its well shaded habitat into the dry hot places where the other two species are found.

I believe that throughout the Cycadales there has been a gradual reduction in the number of sporangia on a sporophyll. On this basis the sequence would be as I have given it.

On the other hand, it must be admitted that in *D. edule* the ovulate cone is not so compact and the megasporophylls have not lost so completely the character of the vegetative leaf, which must be assumed as the ancestral form of both kinds of sporophylls.

Since the original description of *D. spinulosum* was necessarily inadequate and incomplete, it seems worth while to describe the species from the more abundant material now available.

DIOON SPINULOSUM Dyer.—Adult plants 2–16$^{m}$ in height; stem slender, with conspicuous transverse ribs, and a single zone of wood; leaves 1.5–2$^{m}$ long, curved, with 80–117 leaflets on each side; leaflets 15–20$^{cm}$ long, 10–15$^{mm}$ wide, with 5–8 spines on each margin, the lower ones gradually reduced to mere spines; first leaf of seedling with as few as a dozen leaflets on each side, the leaflets with only 2–6 spines on each margin, lower leaflets not at all reduced; ovulate strobilus cylindrical ovoid, 35–50$^{cm}$ in length, 20–27$^{cm}$ in diameter; sporophylls densely hairy, closely imbricate, the exposed portion rounded or obtuse at apex; seeds smooth, white, 4–5.5$^{cm}$ in length, 2.5–3.5$^{cm}$ in diameter; staminate strobilus elongated ovoid, 21$^{cm}$ in length, 10$^{cm}$ in diameter; exposed portion of sporophyll hairy, obtuse; microsporangia about 750 on a sporophyll.

Observed growing wild at Tierra Blanca (State of Vera Cruz) and at Tuxtepec (State of Oaxaca), Mexico.

Material has been collected at intervals and a future account will deal with critical stages in the life history.

THE UNIVERSITY OF CHICAGO

# THE INFLUENCE OF GRAVITY ON THE DIRECTION OF GROWTH OF AMANITA

STELLA G. STREETER

(WITH THIRTEEN FIGURES)

The following account is a record of a series of experiments carried on at the Biological Laboratory of the Brooklyn Institute at Cold Spring Harbor, under the direction of Professor D. S. JOHNSON, during the summers of 1906 and 1908. The object was to determine, if possible, the reactions of some of the common toadstools to the gravity stimulus. The main points under consideration are the promptness and accuracy of the response, the duration of the response after an efficient stimulus, the location of the zone of elongation, and its relation to the responsive zone. The conclusions here stated were drawn from observations made on about 3000 specimens, collected in the woods and replanted where conditions could be controlled. With the greatest care not more than one out of every ten planted yielded a satisfactory record. The agarics break easily, often from their own weight, when placed in a horizontal position; some shriveled instead of developing, and many were infested with the larvae of various insects, which fact was not apparent until the toadstool was near maturity.

The species used in these experiments were *Amanita phalloides* Fr. and *A. crenulata* Peck. These forms were chosen because they have long stipes, because transplanting seemed in no way to retard the normal development, and because they were very abundant. The food supply is stored in the button, so that the plant is not seriously affected by removal from the mycelium. The plants were collected from the woods just after they broke through the ground, at the stage when the pileus is beginning to break through the volva. Each was taken up carefully with some of its surrounding soil, carried to the laboratory, and there planted again in a tumbler. When it had been allowed to rest in the normal vertical position in a dark chamber for a short time, a careful drawing of each specimen was made in the following manner. The plant was placed, with the

stipe horizontal, at an accurately measured distance, before a sheet of paper firmly supported on a vertical drawing-board. In front of the toadstool and always at the same distance from it as the paper was fixed a black screen having a pinhole aperture. The drawing was made by looking through the opening and tracing the outline of the plant as it appeared against the paper. Other records were made in this way from time to time, depending upon the object of the experiment. The plant was in no way disturbed, and these records showed all changes of position in the vertical plane, and from them it was possible to measure these changes in units of angular measurements.

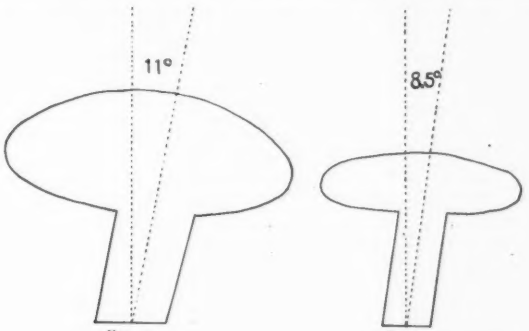



FIG. 1 FIG. 2

FIG. 1. *A. crenulata*, 11° from perpendicular.—FIG. 2. *A. crenulata*, 8°.5 from perpendicular.

A few simple experiments showed that the forms used were positively heliotropic. Specimens planted in tumblers were placed in boxes which were painted black on the inside. One entire side of each box was left open and the boxes were placed in a west window with the exposed side toward the light. After standing in this position for 24 hours, the plants had bent 8° to 12° toward the light (*figs. 1, 2*). In *fig. 1* the main axis of the toadstool is shown inclined 11° from perpendicular, and in *fig. 2*, 8°.5. To avoid light stimulus, all experiments with reference to geotropism were performed within a moist dark chamber, which in turn was kept in a dark room.

After the pileus broke through the volva, it took the stipe about 24 hours to attain its full length in *A. crenulata*, and nearly 36 hours in *A. phalloides*. With a few exceptions this time element was con-

stant. This short period of development necessitated that all observations on one plant should be made within 36 hours.

In those experiments which required that the plant be held in a horizontal position, the tumbler containing the toadstool was supported firmly on a wooden block by a band of tin nailed securely to each side of the block (*figs. 3, 4*). A slender insect pin was placed in

FIG. 3.—*A. phalloides*, in which supra-curvature has been neutralized.

the center of each toadstool as a continuation of the axis of the stipe (also shown in the figures). This pointer made it possible to measure the amount of curvature accurately. After being collected and planted, each specimen was left in the normal position long enough to counteract any stimulation received during its transference and then it was placed on its side in the dark chamber.

Usually the pileus does not become fully extended until after the

stipe has ceased to elongate (*fig.* 5). In 24 hours after the toadstool had reached its maximum height, the pileus expanded and its diameter increased 1.2$^{cm}$. In all cases where the plant was placed on its side after the stipe had reached its full length, but before the pileus

FIG. 4.—*A. phalloides*, from which the pileus, except that part directly above the stipe, has been removed.

had fully opened, the pileus continued to expand; there was, however, no upward bend in the stipe (also shown in *fig.* 5). After the stipe attains its full length there is no longer any response to gravity stimulus.

When a young plant, in which the entire stipe is still elongating, is placed on its side in the dark, the tip of the stipe begins to bend

upward after 40–60 minutes. This curvature is continued for about 24 or 36 hours, depending upon the species, until the tip of the stipe

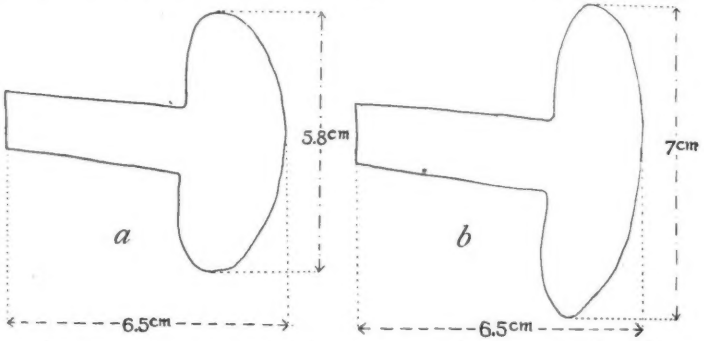



FIG. 5.—*A. crenulata: a*, height 6.5cm, diameter of pileus 5.8cm; *b*, 24 hours later, height 6.5cm, diameter of pileus 7cm.

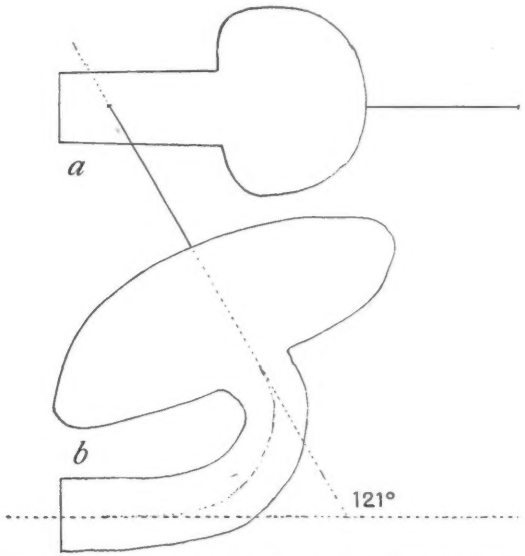



FIG. 6.—*A. crenulata: a*, as planted; *b*, 24 hours later, showing supra-curvature of 31°.

is carried up to and beyond the vertical position, and the original lower edge of the pileus is carried above the horizontal plane (*fig. 6*).

In experimenting with the stem of *Cephalaria procera*, one of the teasels, SACHS (1888) found that this supra-curvature was neutralized

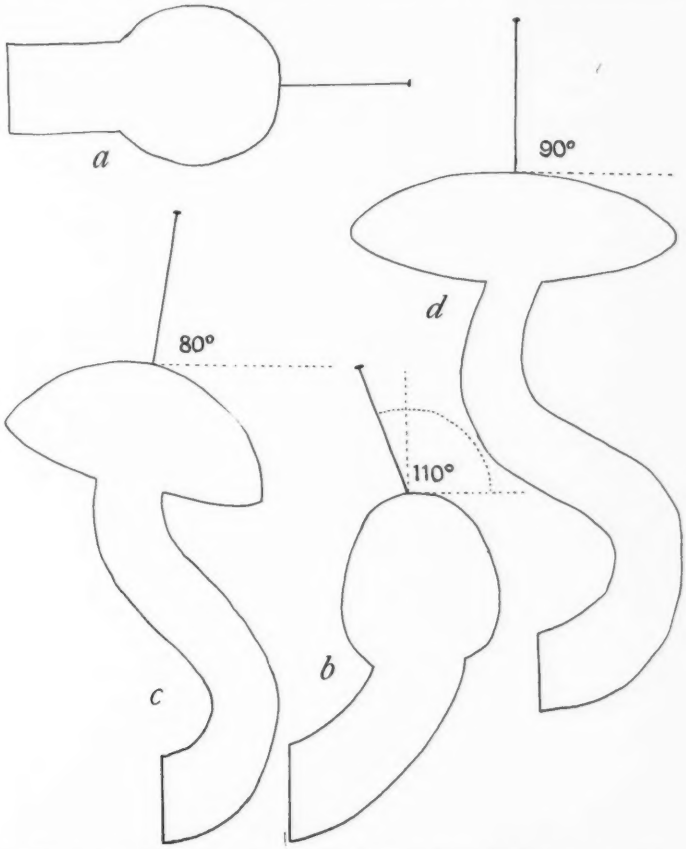



FIG. 7.—*A. phalloides: a*, as planted; *b*, 6 hours later, showing supra-curvature of 20°; *c*, 17 hours after planting, having returned to 10° below vertical; *d*, 30 hours after planting, tip of stipe vertical.

and the stem soon moved back to the vertical position. In the case of *A. crenulata* this supra-curvature is permanent. The probable explanation for this is that the period of elongation is so short that the reaction does not have time to take place before growth ceases.

When young specimens of *A. phalloides*, which have longer stipes and respond more quickly, were used, the tip of the stipe was carried beyond the vertical 2° to 20°, then it stopped and moved back toward and beyond the vertical 1° to 6° on the other side, and by a repetition of this process finally came to rest in the vertical position. *Fig. 7* shows a series of drawings of one specimen of *A. phalloides* in which the supra-curvature was neutralized. *Fig. 3* shows this toadstool just before it came to its final vertical position. This fluctuation only takes place if the plant is still growing when the induced response ceases.

In an attempt to locate exactly the perceptive zone, all the pileus except that part directly above and which forms a continuation of the stipe was removed in the manner shown in *fig. 8*. These plants were then allowed to develop in the dark in a horizontal position for 24 hours, and the result is shown in *fig. 8*. The stipe itself bent, but there was no curvature in that part which belonged to the pileus. This shows that the responsive zone is not situated within the pileus.

The entire pileus was then carefully removed from the tip of the stipe in many plants by a transverse cut where the gills join the stipe. Each specimen was then placed in a horizontal position in the dark and allowed to remain 24 hours. The geotropic response here was normal (*fig. 9*). The stipe, which was bent downward at first, began to bend upward slowly, then more rapidly, carrying the tip beyond the vertical. This shows that the responsive zone is situated within the stipe.

A further attempt to locate the responsive zone was made. Glass tubes were cut in pieces of different lengths and these were placed over the bases of the stipes of plants from which the pileus had been removed. This left 1–4$^{mm}$ of the upper end of the stipe exposed beyond the end of the tube. These tubes were held firmly in a horizontal position by wire, and the plants were kept in the dark for 24 hours. In every case where elongation had not ceased, there was a decided upward curvature of the stipe beginning at the end of the glass tube (*fig. 10*). In this case the stipe was 8$^{mm}$ long, 2$^{mm}$ of this projecting beyond the end of the tube when the experiment was set up. After twenty-four hours the stipe projected 21$^{mm}$ beyond the tube. It had curved upward at the end of the tube, making an

angle of 145° with the position from which it started. This shows that at least part of the responsive zone is very near the tip of the stipe. In other cases, where the stipe had nearly reached its greatest elongation, the result was the same (*fig. 11*). Here the stipe was

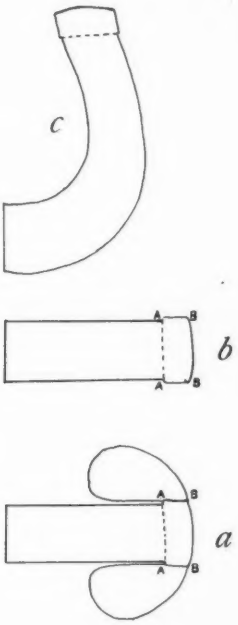



FIG. 8

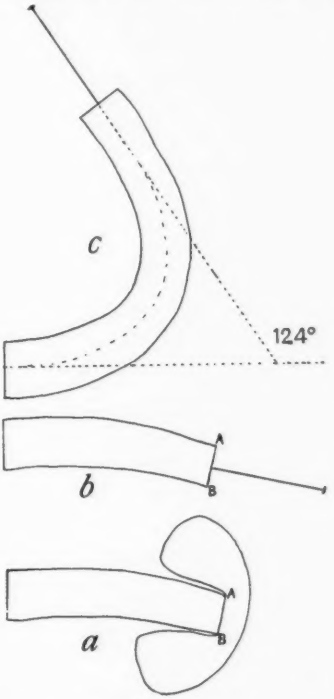



FIG. 9

FIG. 8. *A. crenulata: a*, entire; *b*, as planted, the pileus having been removed as indicated by the lines, dotted lines show depth of pileus; *c*, 24 hours later, showing that curvature takes place in stipe, not in pileus.—FIG. 9. *A. crenulata: a*, entire; *b*, as planted, the pileus having been removed by transverse cut *ab; c*, 24 hours later, showing curvature of 124°.

56$^{mm}$ in length, of which 1$^{mm}$ projected beyond the end of the tube. In this case elongation continued until the stipe projected 3$^{mm}$, and it then showed an upward curvature of 23°. In this case the responsive zone must have been within 1$^{mm}$ of the tip at the start.

In order to determine the distribution of the zone of elongation,

the stipes of a great many specimens in all stages of development were measured. An accurate record of the length of the stipe at the beginning and end of growth was kept. The stipe was marked off into $2^{mm}$ lengths with dots of waterproof India ink. It was possible,

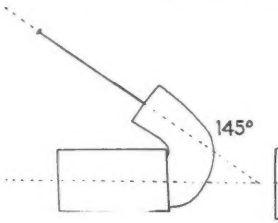



FIG. 10

FIG. 11

FIG. 10. *A. crenulata*, 24 hours after planting; base of stipe held in glass tube; tip curved 145°.—FIG. 11. *A. crenulata*, 24 hours after planting; base of stipe held in glass tube; tip curved 23°.

when growth ceased, to tell in what region elongation had taken place and where it was most rapid. A few of these records are given below.

| Number | Length of stipe at the beginning | Length of stipe at the end | Amount of elongation | Elongating portion at tip | Non-elongating region at base | Elongation in each of uppermost $2^{mm}$ spaces beginning at top | In 2d five $2^{mm}$ spaces | In 3d five $2^{mm}$ spaces | In 4th five $2^{mm}$ spaces | Comparative length of stipe at beginning | Comparative length of zone of elongation | Time |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | mm. | mm. | mm | mm. | mm | mm. | mm. | mm. | mm. | % | % | hours |
| 110 | 7 | 33 | 26 | 7 | 0 | 7–10–5½–3½–0 | | | | 21.2 | 100 | 36 |
| 216 | 20 | 50 | 30 | 20 | 0 | 3–3–3–3–5 | 4–3–2–2–2 | | | 40 | 100 | 36 |
| 218 | 30 | 68 | 38 | 30 | 0 | 2–2–3–3–4 | 4–4–3–3–2 | 2–2–2–1–1 | | 44.1 | 100 | 36 |
| 157 | 40 | 72 | 32 | 40 | 0 | 3–4–3–3–2 | 2–2–1–1–1 | 1–1–1–1–1 | 1–1–1–1–1 | 55.5 | 100 | 36 |
| 104 | 20 | 34 | 14 | 20 | 0 | 1–2–2–2–2 | 1–1–1–1–1 | | | 58.8 | 100 | 36 |
| 142 | 30 | 42 | 12 | 20 | 10 | 2–2–2–1½–1½ | 1–½–½–½–½ | | | 71.4 | 66.6 | 36 |
| 148 | 42 | 52 | 10 | 20 | 22 | 1–2–1–1–1 | 1–1–1–½–½ | | | 80.7 | 47.6 | 36 |
| 138 | 102 | 104 | 2 | 8 | 94 | ½–½–½–½–0 | | | | 98 | 7.8 | 36 |
| 123 | 36 | 36½ | ½ | 2 | 34 | ½–0–0–0–0 | | | | 98.6 | 5.5 | 36 |

The specimens described above were grown in a horizontal position, and the measurements were taken on the lower side. Comparing the length of the stipe at the beginning and at the end of the experiment, and then comparing the length of the zone of elongation with the length of the entire stipe when the first measurement was taken, we find that elongation takes place throughout the entire length of the stipe until after it is 60 per cent. grown. From this time until

growth ceases, the zone of elongation becomes shorter and shorter, but is always just below the pileus. In the specimens used to make out the above table, the length of the mature stipe varied from 36 to 112$^{mm}$, and the length of the zone of elongation varied from 2 to 40$^{mm}$.

Record was made of the amount of elongation which had taken place in each part of the stipe beginning at the pileus. By referring to the table it can be seen that in those plants which are about one-third grown or less, the zone of most rapid elongation is in about the middle of the stipe. As growth continues, this zone moves up the stipe. In plants which are half grown or larger, the zone of most vigorous growth is the second 2$^{mm}$ from the tip. When the zone of elongation becomes less than 4$^{mm}$ in length, growth takes place in the upper 2$^{mm}$ (see record for 123). The elongation within the upper 2$^{mm}$ of the stipe is usually less than that within the second 2$^{mm}$, but in some cases they are equal. The amount of elongation in each 2$^{mm}$ becomes less and less from the point of most rapid growth toward the base, until the growing region is passed.

In order to determine the time element in the geotropic response of these toadstools, plants were placed in a horizontal position in the dark and records of the amount of curvature were taken each hour. The following table gives the records of two of these specimens:

| Time | No. 51 | | No. 56 | |
|---|---|---|---|---|
| | Position | Amount of change for each successive hour | Position | Amount of change for each successive hour |
| 7:30 A. M. | 0° | | 0° | |
| 8:30 A. M. | −4° | −4° | 5° | 5° |
| 9:30 A. M. | 1° | 5° | 15° | 10° |
| 10:30 A. M. | 4° | 3° | 23° | 8° |
| 11:30 A. M. | 8° | 4° | 32° | 9° |
| 12:30 P. M. | 11° | 3° | 42° | 10° |
| 1:30 P. M. | 15° | 4° | 52° | 10° |
| 2:30 P. M. | 19° | 4° | 62° | 10° |
| 3:30 P. M. | 22° | 3° | 72° | 10° |
| 4:30 P. M. | 24° | 2° | 82° | 10° |
| 5:30 P. M. | 26° | 2° | 88° | 6° |
| 6:30 P. M. | 28° | 2° | 92° | 4° |
| 7:30 P. M. | 30° | 2° | 95° | 3° |
| 8:30 P. M. | 32° | 2° | 97° | 2° |
| 9:30 P. M. | 32° | 0° | 98° | 1° |
| 7:30 A. M. | 32° | 0° | 98° | 0° |

In about two-thirds of all the plants placed in a horizontal position in these experiments, there was a bending downward of 1° to 6° during the first hour, before there was any observable upward curvature. This may be partly due to wilting caused by transplanting. In general this downward tendency was less in the younger specimens where the stipe is shorter, and it was less where the pileus had been removed. These facts seem to indicate that it might be the physical effect of a new lateral strain rather than a response to a new stimulus. For this reason in many cases the pileus was removed, as is shown in *fig. 4*. No. 51 shows this bend downward in the first hour, followed by 1° more than complete recovery in the second hour. For the next six hours the rate of curvature fluctuated from 3° to 4° per hour; this was followed by a steady rate of 2° per hour for five hours; then the pileus came to rest at an angle of 32° from horizontal. In No. 56 the response during the first hour was slight; during the second it was greatly accelerated; this was followed by a period of depression which lasted for one or two hours; from this time on for the next five or six hours the reaction was constant and rapid, then more slow. After the vertical line was passed, the curvature took place more and more slowly until, in the case cited here, it came to rest at an angle of 98° from its original position. Nine hours later, or 24 hours from the start, it remained in the same position and there had been no increase in length. There was no neutralization of the 8° of supracurvature.

In order to determine the exposure period, that is, the length of time which the plant must be stimulated in order that reaction may follow, several plants were kept in a fixed horizontal position for 15 minutes and were then rotated on a clinostat about the horizontal axis for 24 hours. The plants gave a decided reaction to geotropic stimulation for this length of time. There was an upward curvature of the stipe varying from 15° to 30° from its position during exposure to the stimulus. Four records of plants of *A. phalloides*, stimulated by being in a horizontal position for 5 minutes and rotated on a clinostat for 24 hours, showed an upward curvature of 7°, 10°, 10°, and 15°, respectively. Eight records of plants of both *A. phalloides* and *A. crenulata* stimulated for one minute all show an upward curvature of either 6° or 7°. In one case of stimulation for 5 minutes,

in three cases of stimulation for one minute, and in all cases (ten records) where the specimens were in a horizontal position only 30 or 15 seconds, there was no direct upward curvature. Instead, the stipe had made a definite spiral curvature in the same direction as that in which the clinostat moved. Clinostats which rotated in opposite directions were used and the spiral always followed the direction of the clinostat (*fig. 12*).

To find the latent period, the pileus was carefully removed that curvature might not be retarded by the weight which would cause a strain in an unusual place and the plants were placed in a horizontal position. Records were made every 10 minutes. In young, vigorously growing specimens, there was an upward curvature observable in 40 minutes. In other specimens which were nearer maturity, the period was longer, in some cases being 60 minutes.

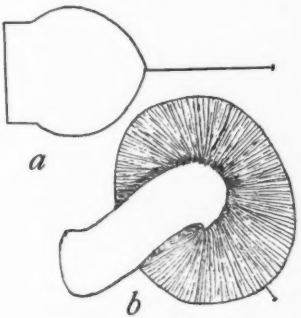



FIG. 12

FIG. 13

FIG. 12. *A. phalloides: a*, as placed on clinostat; *b*, 24 hours later, showing special curvature of stipe.—FIG. 13. *A. phalloides*, showing amount of curvature for each 10 minutes for 80 minutes.

No records which showed the downward bend were considered in this experiment. The diagram (*fig. 13*) shows the rate of curvature in a typical specimen.

## SUMMARY

When young and vigorously growing toadstools were placed with the stipe in the horizontal position, the stipe of each toadstool bent and carried the pileus up to or beyond the horizontal position. This supra-curvature when it occurred was neutralized if growth did not cease too soon.

The responsive zone is situated near the tip of the stipe, not within the pileus.

The stipe elongates throughout its entire length, until it is more

than half grown. The zone of most rapid elongation is always just below the pileus and becomes shorter and shorter until growth ceases.

When placed in the horizontal position, the tip of the stipe curved upward very slowly at first, then more rapidly, until it passed the vertical position, after which the curvature took place more slowly until it came to rest. If growth were still vigorous, the tip of the stipe again passed the vertical, rested on the other side, and finally assumed the ordinary position.

The amount of time which a toadstool must be stimulated in order that reaction may follow is less than a minute. How much less was not satisfactorily determined, probably because the clinostats used rotated too slowly.

The latent period varied from 40 to 60 minutes, the younger specimens responding more quickly.

JERSEY CITY, N. J.

# THE WILLIAMSONIAS OF THE MIXTECA ALTA

G. R. WIELAND

(WITH TEN FIGURES)

The great plateau and mountain region in the central and western portion of the southern Mexican state of Oaxaca is commonly known in Mexico as the Mixteca alta, or high country of the Mixteca Indians. This name is used in contradistinction to the Mixteca baja, or portions of the lower country or tierra caliente over which the Mixtecas have extended. Simply speaking, then, the Mixteca alta is a portion of the southern edge of the Cordilleran system facing the Pacific and extending through western Oaxaca to the border of Guerrero, or into the latter state. Here, during some five months of the past winter and spring I have had the pleasure of continuing field work on the American fossil cycads under the auspices of the Instituto Geologico Nacional de Mexico. I have the kind permission of the director, Señor AGUILÉRA, to note in this preliminary manner that the results obtained are regarded as of the greatest interest to paleobotanists.

The field work has included the making of an accurate section through fully 2000 feet of plant beds of Rhät-Liassic age, full of cycads in as great a variety of types as has thus far been encountered anywhere in the world. Indeed, considering the fine material obtained from the localities noted in the valley of the Rio Nochixtlan near Tlaxiaco, at Mixtepec on the Rio Tlaxiaco, notably all around the Mina Consuelo, about El Cerro del Lucero, and the Rosario region to the southwest of Tezoatlan, as well as elsewhere, and considering, moreover, the almost endless opportunity for opening up quarries in all this extensive country, I am of the opinion that the Mixteca alta is one of the most promising and accessible regions for the student of fossil plants yet discovered.

True enough, these localities are distant from the railway 50 to 150 miles or more, over the roughest of mountain trails. And as mountain succeeds mountain with scarce a valley between, there are some real difficulties for the collector, who must send out his material in blocks of limited size, such as can be loaded on the backs of the

tough little burros, or on the strongest mules, which can carry a pair of boxes of 200 pounds weight each. Hence, it more than once becomes necessary to break the splendid slabs all covered with leaf impressions, and often bearing flowers, which one can secure in even the smaller quarries almost without limit.

But for a country so distant, there are many very distinct advantages and no final obstacles. Animals are trusty; the Indians are good and cheap workmen; one is everywhere met with great courtesy; it is a source of much interest to find the high degree of comfort to be had in some of the most distant of the towns and villages; the food is always good, and even in the far mountains one can always get eggs and tortillas. All in all, if one is only fairly fore-wise, to spend a winter in the sunshine, the forests, and amidst the grand scenery of the Mixteca alta is much more like enjoying oneself in some geological sanatorium, as it were, than like hard work. For the naturalist ever finds a thousand and one points of interest, and soon becomes accustomed to ride 20 to 50 miles a day as he may need; while if interested in the cycads he can find places farther down the cañons and deep valleys where species of Dioon are fruiting hard by strata yielding the fossil forms in profusion.

The great thickness of these Oaxacan plant beds has been noted; but as to their exact age I am not sure, it being as yet early to form a fair conclusion. Glossopteris, rather than merely the sagenopterids, is considered present; and there is also a wealth of taeniopterids of older type, as well as a fine series of stems of a small but distinct lepidodendrid, and many leaves of *Noeggerathiopsis Hislopi* Bunbury. But otherwise the facies is uppermost Triassic, if indeed Liassic genera may not in the end be found to preponderate. A similarity to the Gondwanas of India suggests itself.

But what commands our attention at present, far beyond the precise age of these beds, is the fact that there abound in them in great variety the imprints, casts, and molds of many fruits of Williamsonia, closely associated with Zamites, Otozamites, Podozamites, Pterozamites, Ptilophyllum, and Dictyozamites, fronds as well as seeds. One of the strobili is a mold of just such an ovulate fruit as BUCKLAND figured under the name of Podocarya in the *Bridgewater treatises*, the original of which should be at Oxford, but could not be

found when a search was made for it a few years since, as Professor SEWARD of Cambridge has informed me. Also, there is a considerable number of the large buds inclosed by heavy ramentum-covered bracts of the same size and appearance as those from the Yorkshire coast. One favorable circumstance that has conduced to frequent preservation of the surface characters of the ovulate fruits is the formation by the outer zone of a layer of coal, which while liable to checking affords an excellent indicator for which one may keep constant watch. Furthermore, the close association of these fruits, leaves, and stems, though the latter are not well preserved as a rule, leads to the hope that as the collections come to embrace a wider range of localities, and the data of association come to be better known, more than one restoration of the complete plant can be made. That silicified forms may yet be found is proven by the occurrence of a well-silicified log of a new species of Araucarioxylon.

Especially interesting is the occurrence at Mixtepec on the Rio Tlaxiaco of fruits of small size borne on slender stems, and also those with broad bladelike bracts of thin texture, if they are not indeed sepals or petals. These small fruits, while not preserved in finer details, are abundant, and are quite uniformly accompanied by small, much-branched stems, and by numerous fronds no more than $10^{cm}$ in length; though these may have been bipinnate.

Of primary importance is a single fairly well-preserved impression of a staminate disk from midway up in the plant beds in the main barranca between El Cerro del Venado on the south and El Cerro del Lucero on the north, near the coal outcrops of Mina Consuelo, 15 miles from Tezoatlan. On my return from the Mixteca alta I supposed that I had not found any of the staminate organs of the cycadophytes; although various interesting fruits of seed ferns appeared to be present. But I found on my desk at the Instituto Geologico a letter from Professor NATHORST, dated from England and telling me that he had just visited the Yorkshire coast, where he had succeeded in finding the first definitely recognizable male flowers of Williamsonia, these agreeing essentially with the flower of Cycadeoidea as first discovered in the type of *C. ingens* and described in my *Studies of American fossil cycads*, parts I–IV.

It can be readily understood that I had kept a sharp watch for

such disks during all the field work, and that after reading Professor NATHORST's letter this watch was made closer still while the various specimens were being unpacked, placed in order, and further developed. But not until all this work had been done did I finally, in an idle moment, uncover a staminate disk on a slab from near Mina Consuelo. Then I recognized that a form I had suspected at one time was a disk had been truly such, though poorly preserved. It seems I had not chanced on quite the best disk locality. Better localities will yet be found.

The El Consuelo Williamsonia staminate disk is a reduced campanulate form of the size and general structure indicated in *fig. 2*. As there shown, however, the number of fronds is arbitrarily taken for purposes of interpretation as five, instead of the true number of eight or ten. One cannot be quite sure of the exact number in the specimen. The important structural feature, however, is that instead of a bipinnate frond as in Cycadeoidea,[1] there is a small strictly once-pinnate form, the rachises bearing only two lateral rows of synangia. These, however, are still of the marattiaceous or cycadeoidean size and structure. The component fronds project beyond the disk only to a height of about 1.5$^{cm}$. The basal region appears to be rather thin in texture; but the state of preservation as well as the association with other fruits and leaves all go to indicate that these disks and doubtless those of other species and genera should yet be found in abundance.

There can be no gainsaying the supreme importance of this fossil flower in enabling us to form more exact and adequate conceptions of the course of evolution leading up to and resulting in the present diversity of gamopetalous plants. In describing the flowers of *Cycadeoidea ingens* and *C. dacotensis*, I pointed out that the disk type of cycadophytean flower clearly indicated previous stages with the staminate organs spirally inserted beneath an apical cone or series of likewise spirally inserted megasporophylls, and that readily conceivable reductions and changes in such a primitively organized inflorescence or fertile apex or branch fully indicated the mode of origin of Liriodendron. Whence it followed that the Magnoliaceae

[1] I followed the old usage of calling these fronds pinnate in my descriptions; but ARBER has called them bipinnate forms. It seems rather more correct so to do.

must be among if not the most primitive of all the angiosperms. In this I believe I was clearly the first; though HALLIER soon independently reached similar conclusions as to the origin of the Magnoliaceae, and likewise cited Liriodendron.

Later, ARBER and PARKIN visualized in the *Annals of botany* the conception of a primitive semi-cycadean angiosperm ancestor with its crown of reduced, once-pinnate, spirally inserted microsporophylls surmounted by similarly set carpophylls; and these authors at the same time carried much further the idea that the true mode of angiosperm evolution, so long completely hidden, was at last indicated in all its broader outlines by reasonably direct evidence.

In ARBER and PARKIN'S ancestral stage we certainly behold a very primitive and decidedly plastic type, which they choose to call a hemiangiosperm, though I perversely prefer to group such plants under SAPORTA'S old term of proangiosperm.[2] It is one of the hypothetical forms, moreover, which is not only so readily conceivable as undergoing an infinity of modifications in the direction of higher forms, but one which, as I have long since told ARBER, we may confidently expect will yet be found in the fossil stage.

Despite all this progress, the actual mode of modification leading into the more complex types of angiospermous flowers has remained

[2] From a long letter that ARBER has been kind enough to write me, I know his views on the question of whether in hypothesizing the more immediate angiosperm ancestors we may use the old term proangiosperms, or must define a new and different group, the "hemiangiosperms," as he has proposed. I duly respect these views and think it is of importance that they receive a more thorough consideration than can be accorded them here.

At the same time, I wish to point out that we should duly honor SAPORTA as one of the pioneers, who, whether clearly or not, glimpsed an important truth when he placed Williamsonia among his proangiosperms. To claim that the proangiosperms of SAPORTA, as a great and more or less hypothetical group, either had to be, or in his day could have been delimited would to my mind be both impractical and unjust. Moreover, the important point is that we may well allow that SAPORTA was taking a glance backward in the direction of primitive forms even more than forward. Indeed, it is both fair and convenient to remember that the proangiosperms, as a great group leading into the angiosperms, could have their gymnosperm section, and yet logically include other truly lineal families, these being of hardly more than family distance from the Cycadeoideae at best. For these reasons, partly pertinent at least it seems to me that to use fairly the term hemiangiosperm we must go much farther back, to where by another hiatus the proangiosperms merge into the more primitive fern derivatives.

obscure. While SCOTT, especially, as well as HALLIER, ARBER and PARKIN, BESSEY, and others, as well as myself, have all insistently urged that the path has thus really been blazed to a knowledge of the evolution of the angiosperm groups, no one has yet been in a position to bring the final methods more clearly into view. Now, however, I believe we can do so in the case of all but the extremely modified families, if not indeed ultimately in these too, by means of analogic methods combined with comparative morphology.

We have seen how the staminate disk of *Cycadeoidea ingens*, and of all the other species so far known, bears inside the campanula or androecium many functional synangia on the rachial axes, either inserted directly or on pinnules. Now we see, furthermore, that the campanula remains large in a form with greatly reduced fronds, while we may be sure that interiorly borne synangia are still present on the rachial axes, or at least may be in related forms, whether we can detect them or not. Whence it follows that a slight further continuance of the rachial reduction, so plainly under way, must result in a toothed campanula bearing interiorly on each axial or rachial line only a single pair of synangia and finally a single synangium and no more, just as diagrammatically shown in *fig. 3*. Such types we may call, because of the strictly convolvulaceous aspect, *archaeosolandrous*, arbitrarily dismissing for the present all mention of the central ovulate region to which we return below.

Now plainly, having thus by a series of entirely simple stages reached this archaeosolandrous form, which we confidently believe will be detected in the fossil condition, it is only a minor step to simpler types of pollen sacs, either borne in pairs or singly, and finally to elongations of the filaments suiting the requirements of such flowers as that of *fig. 4*, which is none other than a common morning glory.

In short, the successive members of the series of steps outlined are these, letting capitals represent the known, and small letters the hypothetical plants:

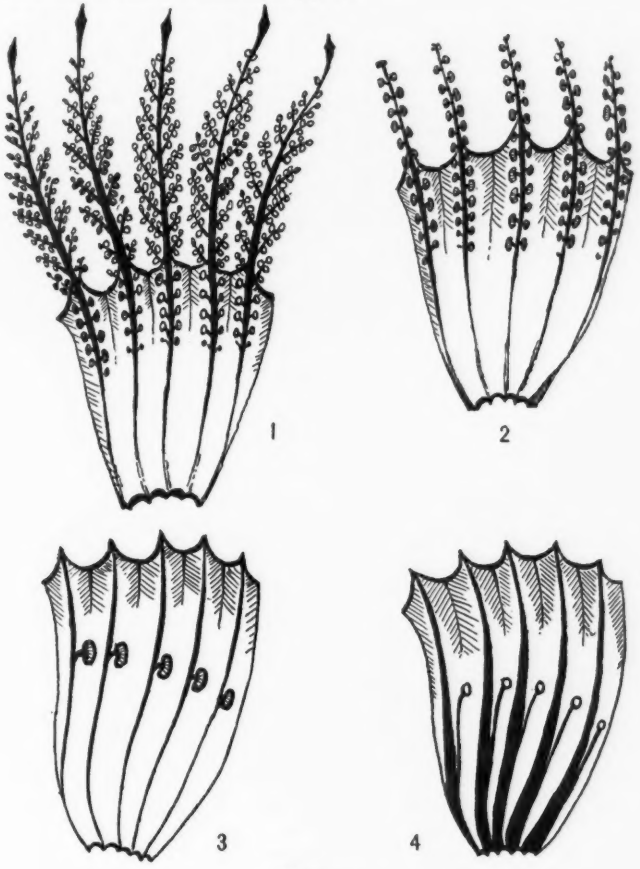
*A'*. Proangiosperms, or hemiangiosperms and pteridosperms.

*A*. The flower of *Cycadeoidea dacotensis*, with a campanulate disk of 18 bipinnate members.

*B*. The flower of *C. ingens*, with 12 bipinnate members.

*C.* The flower of *C. Jenneyana*, with only 10 bipinnate members, as well as various other greatly reduced and small types of flowers of Cycadeoidea.

*d.* A hypothetical flower of Cycadeoidea, with a staminate disk of 5 bipinnate members or staminate fronds (cf. *fig. 1*).




FIGS. 1–4

*E.* The El Consuelo staminate disk composed of 10 or 12 pinnate fronds.

*f.* A derivative of the El Consuelo disk, with only five pinnate fronds forming the campanula (cf. *fig. 2*).

*g.* A hypothetical campanula derived from the preceding by reduction of the synangial number to two and finally one, borne interiorly (*fig. 3*).

*h*. Unknown intervening plants derived from *g* and undergoing reduction in the number of the sporangial loculi, with thinning of the synangial wall, or

*i*. An unknown form much like *g*, but with a simpler type of pollinial organization. (This is the more probable member of the direct series, but both may be conceived of as having once existed.)

*j*. A campanula derived from either *h* or *i*, in which reduction to the angiospermous pollen sac has taken place, and in which elongation of the staminal pedicels or filaments is going on (cf. *fig. 4*).

*K*. The staminate campanula of the convolvulaceous and many other gamopetalous flowers.

Thus may we derive the staminate zone of gamopetalous forms by a series of readily conceivable and closely united reduction stages, the principal members of which are in the larger sense already known. But let us now see if it be possible to go on and establish a plausible ovulate correlation; for if this cannot be done it is more than superfluous to say that *K* is in the extended sense not proven to be a true member of the evolutionary series *A'*, *A–j*.

That an apical series of spirally inserted carpophylls giving rise to a central ovulate cone played the chief rôle in the development of the Magnoliaceae, as in all the conifers and doubtless many other forms, is evident enough. But that such a cone was in *all* cases organized, or much less that a terminal group of diffuse carpophylls was present in all the ancestral phyla of the angiosperms, is after a little consideration seen to be a cumbrous hypothesis. By what other means then than by the reduction of the carpophylls and of cones may we conceive of the cognate origin of the ovulate region in angiosperms?

Perhaps the Draceneae may be made to give an initial answer. Take for instance the cultivated maguey (Agave) of Mexico, with its six immense versatile anthers borne on their long projecting filaments as seated in the interior surfaces of the six fused sporophylls, three of which are smaller, and the other three of which are alternately of larger size. On cutting this flower open and viewing it from the interior, is not the structure in reality that very diagrammatically indicated in *fig. 5*?

Now, was not this floral structure derived from a consolidating and changing whorl of six primitive bisporangiate fronds with basal megaspores and apical microspores? The simple method of deriva-

tion from such a primitive, or *archaeo-amarillidaceous* plant would consist in basi-lateral fusion of the sporophylls and development of a trilocular ovary, with the synchronous reduction and change of the microspore zone to the series of six interiorly borne stamens, after the manner shown to be feasible in the above series *A'*, *A–j*. Such we conceive to have been the origin of the yuccas and agaves; for it is no more improbable that heterospory should in many primitive stocks arise thus regularly in each of an apical whorl of sporophylls, than that it should find expression in the segregation of a basal group of megasporophylls followed by an apical group of microsporophylls, as in Cycadeoidea.

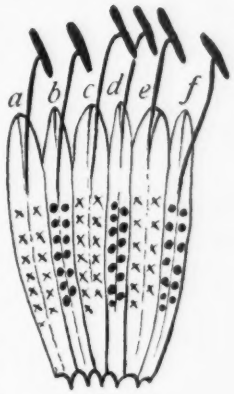


FIG. 5

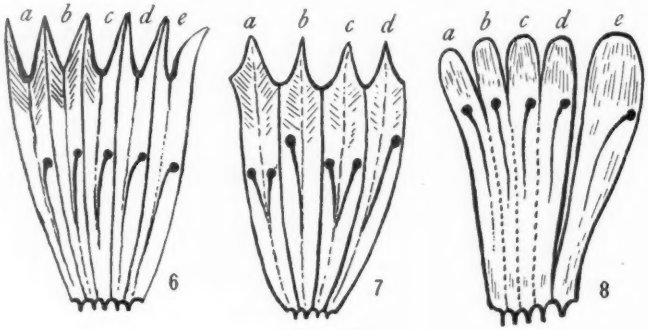
Evidently in *Agave americana* the last stage of fusion resulted in the suppression of the basal or megaspore region of three alternate fronds. Nor is it so difficult to conceive how, the plant finding the inclosure of the ovarian region to its advantage, an elongation of the style finally resulted, with the retention of the gametophytes and seeds. Also, the long filaments must have been very readily produced by the flower under the stress of impulses that had to do with nothing else than the ordinary phenomena of fertilization. Such, surely, are the conclusions one may reach from the macroscopic examination of flowers like Agave and perchance likewise of the rose hip.

While the manner of evolution just outlined is in reality not utterly different from that of the Magnoliaceae, the order in which the parts are segregated clearly indicates a remote separation of the several stocks involved, and therefore the virtual polyphyletic origin of the angiosperms. But of course, when the initial changes, and when the major or crucial changes leading up to the two groups now considered so briefly, took place, and which group is in reality the more ancient, are questions that only the future may answer.

Having seen that the ovulate region, whether locular or strobilar, and whether there are few or many ovules, offers no impassable

hiatus, it becomes desirable to interpret a few more examples of staminate organization leading toward or into the more complex types of flowers. Thus may we best test our theory and see if it applies to petals and stamens generally, and really affords a far-reaching explanation of floral constitution in the angiosperms, with ultimately a better basis of classification. But in so doing we may only take up a few forms; for an exhaustive analysis of the families based on the necessary histological and developmental data must be a truly gigantic task for many years and many workers.

Various gamopetalous flowers have the structure shown in *fig. 6*. Apparently the stamens alternate with the lobes of the corolla in




FIGS. 6–8

such forms; but on closer examination it is seen that in reality the axis of the component leaves has shortened to form the notches. This difference, so convenient in classification, therefore rests on very slight anatomical distinction, unless it can be found to accompany a particular juxtaposition of the ovules throughout the groups in question. My example is from a shrub I found growing on the slopes of Popocatepetl, though anyone may turn to Gerardia and Pentstemon as equally good examples of this type of androecium.

Again, the cruciform flower invites attention, whether it be regarded as an approach toward or a departure from distinctly gamopetalous types. For in the cruciferous flower, although the stamen is apparently inserted on the common receptacle, rather than as in the diagrammatic *fig. 7*, there is considerable doubt if it is to be regarded as of discrete origin. Instead, it would seem more probable that

although the point of stamineal attachment has become strongly depressed and indeed is virtually basal now, the flower has arisen very similarly to that shown in *fig. 4*. The two single stamens alternating with the two pairs thus form an opposing analogy to the suppression of megaspore regions in the Agave. But other explanations are also possible. For we believe that in the angiosperms petals have developed from bracts, that they have resulted from the complete sterilization of sporophylls, and that, as explained above, they result in vast numbers of instances from the apical expansion of a sporophyll, which, though greatly reduced, may still bear either megaspores or microspores or both.[3] And furthermore, we regard the stamens of Liriodendron as final reduction stages of individual sporophylls that were once large.

Of further interest in the cruciferous flower is the fact that little or no difference in the development of the petals accompanies the staminate change. But, on the contrary, in the diagram of a honeysuckle (*fig. 8*), while the stamens are of normal number and size,

[3] There also appear to be various instances of more or less completely salver-shaped corollas, in which what are usually called the sepals are in reality fertile organs alternate with the petals, between which they press and fuse up to the beginning of the lobes of the corolla, and there bear stamens just as do the petals. Take for instance those forms with four "sepals," four petals, and eight stamens borne four on the petals and four alternately between them, but plainly scaling off with the members of the calyx. The cherry (*fig. 9* from GRAY) is perchance yet another example, but one retaining more stamens, these not being so distinctly determinate in number. (They may all be of the inner row.)

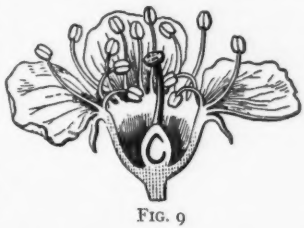


FIG. 9

Perhaps as great a difficulty as we meet anywhere in applying these hypotheses of floral structure is in the case of a form like Silene with discrete hypogynous stamens and a free multiovulate ovary with an apparently distinct axial relation, for here there are several possibilities. Naturally that first coming to mind is that of a central carpellary whorl, followed below by a staminate whorl, and then by the members of the floral envelope. But another method needs to be reckoned with, namely, that which may be briefly characterized as a completed supero-axial shortening and consolidation of the bisporangiate fronds of an apical whorl, in such manner that basal megaspore-bearing pinnules assumed a vertical position and fused to form the ovary, style, and stigma, while the more apical microspore regions of these same fronds produced the stamens, the frond tips finally forming the corolla.

the members of the corolla undergo division into a major and minor group. And plainly, from these simple phases we may no doubt ultimately pass by as simple steps and combinations to a reasonable interpretation of all the multifarious reductions, suppressions, and alterations in first one set of organs, and then another, resulting in papilionaceous, orchidaceous, and all the manifold forms of angiospermous flowers.

It is obviously not feasible adequately to show the derivation and the complex relations of sporophylls leading from the primitive to the higher types in any simple manner. Above all is this true because of the necessity of taking into account the varied possibilities and phases of monoecism and dioecism in any even approximately complete presentation. And the different rates of reduction at different periods, we are bound to assume, further complicate the problem. Indeed no one diagram and no one set of diagrams would serve to outline adequately the changes now suggested. Nevertheless, the attempt is made in *fig. 10* to give the simplest and most abbreviated expression of sporophyll change possible.

Have not the transformations really been easier than we think? Dictyozamites, the net-veined cycad, and many net-veined ferns of which some were doubtless seed-bearing, together with the forms of unknown fruit like Cissites, Vitiphyllum, and Liriodendropsis, all go to show that there is no special hiatus between the angiospermous foliage and the more primitive seed-bearing plants. A single new locality in the upper Triassic or lower Jurassic may at any time completely close the foliage gap. Again, the stem structure of the angiosperms presents no difficulty of derivation from the older types, in which free branching is already known, as well as the presence of numerous flowers undergoing great reductions and changes.

The great double funnels of the near-by Ipomoea, nearly a foot in length, show how readily fusions have gone on, and how great must have been the changes, reactions, and alterations going on for ages in all floral organs. The balance once disturbed, or a critical stage or plastic form once accomplished, infinite changes in a truly polyphyletic race set in.

Other fossil evidence for metamorphosis and reduction will be forthcoming, and speedily. But the student of fossils now realizes

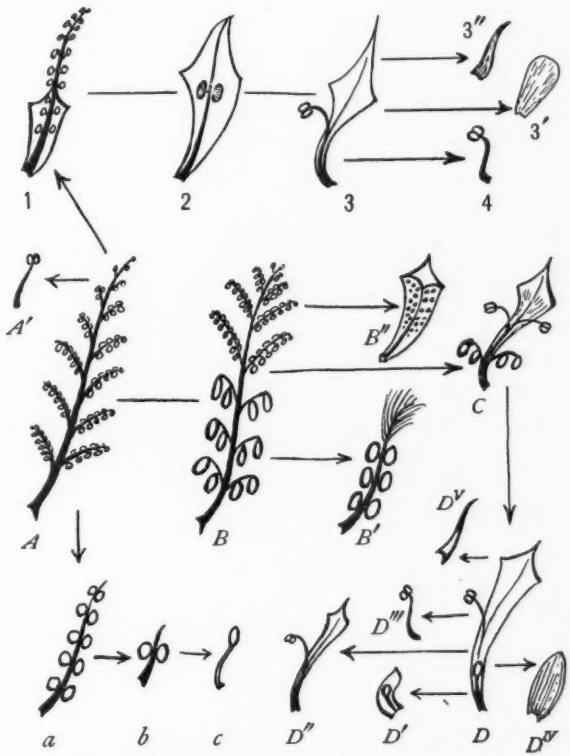



FIG. 10.—Theoretical and actual stages in the development of megasporophylls and microsporophylls of existing spermatophytes from hypothetical homosporous fronds.

*A*, homosporous early pteridophytes (Paleozoic); *B*, heterosporous pteridophyte derived from *A* (Permian?).

*B′*, carpellary derivative of *B* (Permian; Cycas); *B″*, staminate derivative of *B* (Permian?).

*C*, reduced form of *B* and a progenitor of gamopetalous angiosperms; *D*, further reduction stage of *C*, with potency of giving rise to all the essential organs and parts of a perfect flower; $D^{I-V}$, the stamino-petal (*D″*), carpel, stamen, petal, and sepal successively derived from *D*.

*a*, true carpellary leaf; *b*, reduced carpellary leaf; *c*, pedicellate ovule or seed (Cycadeoideae).

1, true staminate frond (Williamsonia, Cycadeoidea) of type leading to gamopetalous angiosperms; 2, true reduced staminate frond; 3, true stamino-petal; 4, stamen; 3′, 3″, second method of sepalo-petalous derivation.

GROUPS AND COMPLEXES.—$B'+B''$ (I–IV) = Cordaitales, Coniferales, Ginkgoales, Cycadales; $A+C$ (V) = Cycadeoideae and many proangiosperms; $A'+C$ (VI) = Magnoliaceae, Liriodendropsis, etc.; $A'+C$ (VII) = many types of naked flowers; $C+D$ (VIII) = gamopetalous and convolvulaceous forms; $D'+D''$ = many angiosperms; $A+a$ = proangiosperms.

that the proangiospermous or hemiangiospermous plant types which will exhibit critical developmental phases are likely to be inconspicuous, and that they must be studied with extreme care. Our hypothetical archaeosolandrous type, for instance, could be very easily missed, though found in excellent preservation. It will be necessary for that fortunate collector who finds the horizon and locality with lineal members of the early angiosperm line imbedded in it, to apply to his material all the newer laboratory methods, namely: (1) the staining, imbedding, and sectioning method used by JEFFREY and HOLLICK in dealing with forms apparently more like impressions or carbonaceous material than the partly preserved structures such as they finally found; (2) the developmental method, by means of which BEECHER showed the preservation of the most delicate trilobite structures, and won such clear results; (3) the collodion method of NATHORST for recovering microscopic surface details, which are often present.

That intermediate types will be found in increasing number cannot be an idle prediction. That from time to time there will be found types definitely hypothesized, may be hopefully expected. Ten years ago I predicted the discovery of the seed ferns, now known in such number and variety. Even then it had become clear that "progressive prothallial elimination with correlated spore differentiation and alteration of the frondlike sporophytes of primitive ferns of the marattiaceous or an allied group were the basal factors in the evolution of the cycadofilicinean and cordaitean alliance." And it already seemed probable that the angiosperms could be added in this statement.

At the present time these groups seem to present more and more distinct points of contact, though in a very complex manner, apparently calling into requisition nearly every thinkable modification of the monosporangiate and bisporangiate frond, both on the same and on separate axes, and with nearly every conceivable variety of rearrangement, reduction, sterilization, and suppression. Even in the Cycadales, the better known of which form a really compact group, we have been compelled to say that the orders "do not appear to have passed through precisely the same evolutionary sequence of heterospory, bisporangiate or monosporangiate, monoecious, and finally doecious fructification."

And once more, we are compelled to hypothesize an extensive and far-reaching polyphyly for the angiosperms. But, none the less, the thought is also present that once an approach has been made along all the available lines of evidence, this seeming maze of possibilities may in the end be found vastly simpler than one can now picture. At least we are already persuaded that the day will come when the true relationships and derivation of every angiospermous family will be worked out and satisfactorily stated with mathematical precision.

El Instituto Geologico Nacional
de Mexico

# SAP PRESSURE IN THE BIRCH STEM

## PART I

H. E. MERWIN AND HOWARD LYON

(WITH FIVE FIGURES)

During the seasons of 1902 to 1904 sap pressure observations were made on several kinds of trees in the vicinity of Oneonta, in central New York. Birches and maples illustrate the two extreme types of sap pressure phenomena. Our observations on the maples are in accord with those of other observers, especially as set forth by JONES, EDSON, and MORSE.[1] Sap pressure in the birches has not been studied much hitherto, except as incidental to other studies.

We found that glass tubes of small bore filled with mercury made very sensitive pressure gauges, especially if the tap hole in the tree and the connecting tubes were filled with water or sap when the gauge was attached. When pressure was negative (suction), a bulb tube was sometimes arranged to allow water to flow into the tap hole, and to catch the gas which escaped. Gas in the tap hole when pressure is negative causes disturbing capillary effects. Gas in the tubes has a damping influence upon the gauge.

### Characteristics of sap pressure in the birches

No sap will flow from tap holes in the stem of the birch or ooze from cut twigs till the ground has thawed considerably in the spring. It is not necessary, however, that the air temperature be continuously above the freezing point before pressure becomes high. From April 5 to April 22, 1904, we have recorded seven nights in which the temperature was below freezing; yet on April 5 a positive tension of $44.3^{cm}$ was observed in a yellow birch (*Betula lutea*); April 9, $87^{cm}$ in a black birch (*Betula lenta*); April 18, $35^{cm}$ in a black birch. Freezing nights were often accompanied by negative pressure which was maintained for a few hours after sunrise. The maximum pressure comes about a month after the first decided appearance of pressure. The buds by this later time have begun to unfold. There is at all

[1] JONES, C. H., EDSON, A. W., AND MORSE, W. J., The maple sap flow. Vt. Agric. Exper. Sta. Bull. 103. 1903.

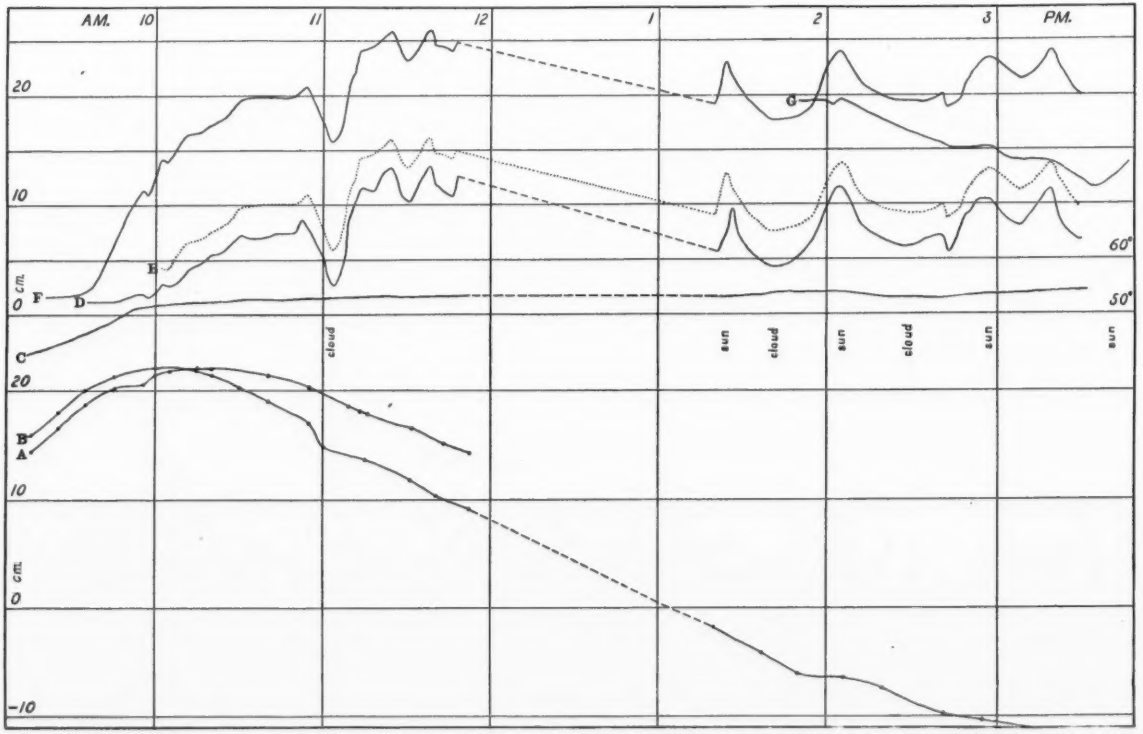



FIG. 1.—Sap pressure curves for maples and birches April 18, 1904: *A*, near the base of a 12-inch maple; *B*, 157$^{cm}$ above *A*; *C*, the shade temperature; *D*, 180$^{cm}$ from the base of 7-inch black birch; *F*, 135$^{cm}$ below *D*; *E* shows where the pressure curve of *D* would have been if there had been exact hydrostatic equilibrium within the tree; *G*, curve for a 10$^{cm}$ maple; the responses of pressure to sunshine and cloud are to be noted.

times a very regular distribution of pressure in the birch trunk, taps at the same height giving like pressures, and taps at different heights showing most pressure in the lowest. The difference between the pressure in the lowest tap hole and that in the highest is usually slightly greater than the hydrostatic difference in level between the holes (*fig. 1*).

Pressure in one hole is always immediately and markedly lowered by sap flowing freely from another hole, even though the holes are on opposite sides of the tree and many feet apart vertically. This fact, of course, indicates a free intercommunication among the ducts of the birch wood.

In all of the cases we have observed, pressure began to be evident at the base of the tree first, and as pressure increased there it showed itself higher and higher up.

Daily fluctuations of pressure in the birch were reported by CLARK.[2] The general character of these fluctuations was brought out by our observations in April 1904. A rapid rise of pressure beginning in the morning is followed by a slow decline till near sunset, then a gradual rise is kept up during the night. The nightly rise of pressure is checked if the temperature of the tree falls below freezing. Changes of pressure are only slight the next day after a freezing night, unless the air temperature reaches 40° to 45° F. or more. (These oscillations of pressure occupying a period of a day are graphically shown in *fig. 3* of the second part of this paper.)

The most striking phenomenon of the birch sap pressure is its variability during those rapid changes of sunshine that take place on days when cumulus clouds occasionally drift before the sun. We have seen the mercury column in a gauge move more than $2.5^{cm}$ vertically in a minute in response to a change of less than 1° C. as registered by a blackened-bulb thermometer exposed to the sun. Furthermore, pressure changes of this rapidity have been kept up for nearly ten minutes at a time. *Fig. 2* is a record for part of an afternoon in which bright sunshine and dense cloud-shadow alternated. A drop in pressure of $37.5^{cm}$ of mercury during a period of cloud-shadow, and a subsequent rise of $30^{cm}$ when the sun appeared, took place between 2:30 and 3:20 P. M. A comparison of the birch

[2] CLARK, W. S., The circulation of sap in plants. 1874.

with the maple, in respect to pressure and the passing of clouds, may be made from *fig. 1*. Even the most decided ups and downs in the curve of the birch pressure are scarcely more than suggested by the slight steepenings or flattenings in the long slopes of the maple curve.

We have always found the maximum pressures in large birches higher than in small ones. The highest pressures observed in both large and small trees were on May 2, 1904. A $7.5^{cm}$ black birch then gave a record of $91^{cm}$ (1.2 atmospheres), a $17.5^{cm}$ black birch of $146^{cm}$ (1.9 atmospheres), and a $35^{cm}$ black birch, about $20^{m}$ high, the astonishing pressure of $204^{cm}$ (2.68 atmospheres). The last pressure would doubtless have been even greater if it had been taken two hours earlier, for both the $7.5^{cm}$ and the $17.5^{cm}$ trees had already declined more than 10 per cent. from maximum when the large tree was tapped. As it is, this pressure is equal to $200^{cm}$ of mercury or $27^{m}$ of water, being $1.8^{m}$ of water higher than any previously recorded sap pressure (CLARK, *l. c.*) Such pressure would support a column of water $7.8^{m}$ higher than the tree. The highest point on the pressure curve of *fig. 2* represents this pressure.

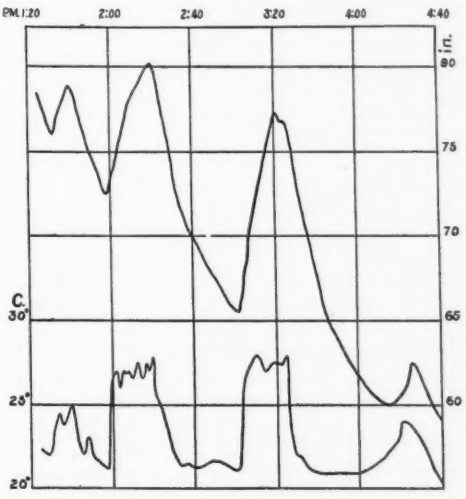



FIG. 2.—The intensity of the sunshine as measured by a blackened-bulb thermometer and the concurrent pressure, measured in inches of mercury, at the base of a $35^{cm}$ black birch, May 2, 1904.

Negative tensions occur frequently in the higher parts of the trunk of the birch, and less frequently near the base. In the latter position it is only in the early part of the season that suction is kept up for more than a few minutes at a time. On April 22, 1904, suction prevailed all day in yellow and black birches that had been in states of

high pressure on several occasions since April 5. A hard freeze the night before and a temperature not exceeding 40° F. during the day seem to have been the chief factors controlling the negative pressure.

### The chief characteristics of sap pressure in the maple

On some warm winter days, at least as early as February 1, sap will flow in amounts of a few cubic centimeters from tap holes in small maples that are exposed to the sun; but the maximum flow and corresponding pressure do not occur till the ground is thawing in the spring. At this time pressures in a tree are not distributed with any apparent regularity. Portions of the trunk at the same level may give very different pressures, and for different heights the pressure may be greatest in either the highest or the lowest situation, though usually pressure decreases irregularly with height (*fig.* 1, *A* and *B*).

Pressure in one tap hole may be but little decreased by sap flowing freely from another hole a few inches at one side of it, but there may be a decided drop in pressure if the flow is from a hole a few feet above or below the hole to which the gauge is attached. From these facts it may be inferred that the ducts of the maple communicate with some freedom along the grain of the wood, but scarcely at all across the grain.

When pressure begins it may be manifest first either near the roots or in the branches, but for any given place in the trunk there is a strong tendency toward a daily increase of pressure during the morning hours, and a decrease during the afternoon. The decrease often goes beyond zero to a considerable suction (*fig.* 1, *B*, after 1:00 P. M.). Size of the tree, situation, and depth of tapping all affect the character of the daily pressure variation. Small size, exposure to the sun, and shallow tapping are all favorable to extreme and rapid pressure changes. In spite of all the variations already discussed, there is a tendency toward parallelism of the pressures developed in different parts of the same tree, and in various trees during a daily period. The causes of such pressure variations, as related especially to daily periods of temperature change, have been discussed by various writers.

There is a general agreement that rises and falls of temperature

of a few minutes' duration have almost no effect upon pressure in the maple. The Vermont *Bulletin* records one instance when a wavy line given by a recording gauge was probably due to variations in sunlight, pressure falling slightly when a cloud obscured the sun. Our record of April 18, 1904, shows conclusively that maples may respond notably to variations in sunlight. In *fig. 1*, lines *A*, *B*, *G* are pressure curves for maples. At 11 A. M. and at 2:00 and 3:35 P. M. the irregularities in the curves were observed to be directly related to insolation. As to the amount of tension that has been observed in maples, our highest records were from a $25^{cm}$ tree March 12, 1902, $75^{cm}$, and from a $10^{cm}$ tree April 5, 1904, $69^{cm}$. The Vermont *Bulletin* (p. 75) records a pressure equal to $129^{cm}$ on March 21, 1898. Pressures exceeding $75^{cm}$ are only occasionally observed. Negative pressures seldom exceed $20^{cm}$.

## PART II

H. E. MERWIN

### Causes of sap pressure variations in the birches

The studies of 1906–1908 were carried on in Cambridge, Mass., in the hope of getting more data as to the causes of pressure variations in birches.

The character of both the long and the short period oscillations on the pressure curve, and the corresponding record of a freely exposed blackened-bulb thermometer for several days, are shown in *fig. 3*. Several important relations are to be noted between the two curves. During the day there is a close parallelism; at night the pressure curve rises regardless of temperature. In other words, maximum pressure and maximum insolation occur at about the same time, near the middle of the day; but minimum pressure comes near sunset, while minimum temperature is nearly 12 hours later, shortly before sunrise. Some of the factors in the control of sap pressure are brought out in the several experiments and discussions that follow. The details of the longer experiments referred to in the general discussion are given under a later heading.

Experiment shows that during the sap season for the birch, all the intercommunicating cavities of the roots and stem are kept practically full of sap. One tree (*exp. 1*) gave the calculated gas

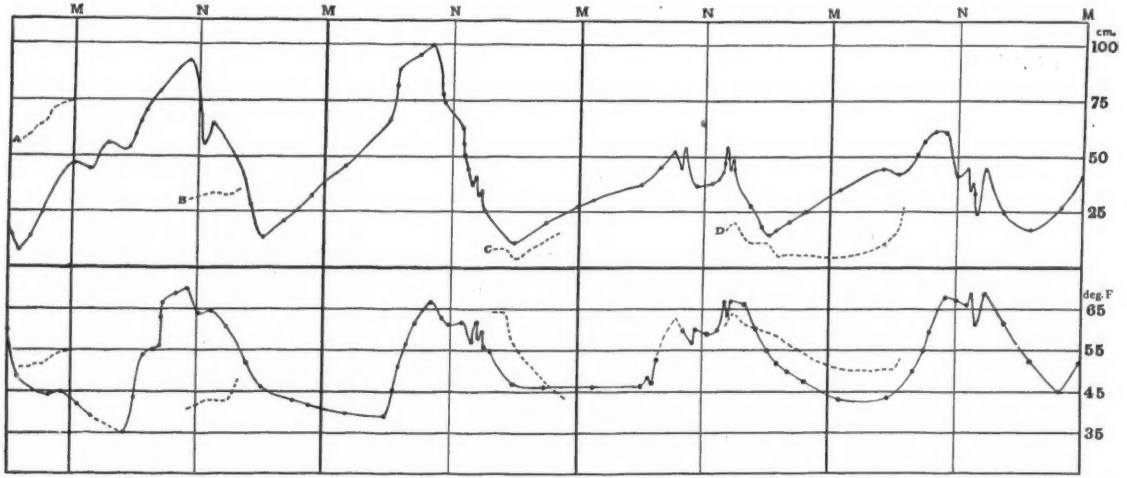



FIG. 3.—The upper curves are the records of pressure in a white birch 11cm in diameter; the continuous line covers the period April 18–21, inclusive, 1906; and the dotted lines *A*, *B*, *C*, *D* are partial records for April 14, 23, 28, 30 respectively; after April 18 the pressure was somewhat lower than it would otherwise have been, owing to a continuous slight flow of sap from the tree; the lower curves are temperatures in the sun; *M*, midnight; *N*, noon.

content of the vessels as about 1 per cent. of the total volume of the vessels. This fact easily explains the state of hydrostatic equilibrium which observation shows to exist in the birch stem when pressures are high. Increasing pressure must diminish the size of gas bubbles to a considerable extent by increasing the solubility of the gas in the sap; decreasing pressure would have an opposite effect.

There is, however, until rather late in the sap season, a good deal of gas in the closed cavities of the wood fibers. This is shown by specific gravity tests. A density of 1 is not attained in the wood of the branches until the buds are about one-third longer than in their winter condition. The maximum density of 1.14 to 1.17 is reached when the first leaves are about $8^{mm}$ long, near the end of the sap season. About a month is required for an increase of 25 per cent. in density. Therefore, the aerial parts of the tree considered in *exp. 1*, with an estimated volume of $57{,}000^{cc}$, would require about $500^{cc}$ of water as a daily supply from the roots to bring about this increase in density.

To get an idea of the amount of water required to maintain evaporation from a tree at the middle of the sap season, two twigs, weighing $1.94^{gm}$ and $2.3556^{gm}$ respectively, after the cut ends had been sealed with balsam were exposed for 3 hours, the first to a temperature of 70° F. in the laboratory, the second to about 42° F. in a breeze. The first twig lost $0.0381^{gm}$, and the second $0.0256^{gm}$. An average evaporation of $0.01^{gm}$ per hour for a twig weighing $2^{gm}$ may be taken, therefore, as an approximate measure of evaporation from the birch for the middle of the sap season. The tree of the experiment bore about 2000 such twigs, from which the evaporation at this rate would be $480^{cc}$ of water per day.

This water evaporated from the tree and that absorbed by the wood fibers during the increase of density of the tree may be taken as the approximate amount of water supplied to the tree daily by root absorption.

Inasmuch as pressures are freely transmitted throughout the birch stem, it is evident that *variations in the rate of evaporation and infiltration and of root absorption*[3] *will cause variations in pressure.*

[3] LIVINGSTON (The rôle of diffusion and osmotic pressure in plants. 1903) has discussed the factors concerned in the control of absorption and pressure in roots.

It is needless to enumerate the weather conditions which affect the rate of evaporation, but it is worth while to note at least one chief factor in the control of root absorption. It is well known that root absorption is accelerated by moderate increase of ground temperature above the freezing point. It has been shown by MACDOUGAL[4] that ground temperatures in the vicinity of New York City at a depth of $30^{cm}$ are maximum about 8:00 to 11:00 at night, and minimum about 8:00 to 10:00 in the morning. At greater depths the maximum and minimum would occur later, but the temperature variations would be less marked. Therefore the maximum temperature of the roots of birches—which lie mostly within less than $60^{cm}$ of the surface of the ground—must occur during the night, and the minimum temperature during the afternoon. Thus, root absorption and the pressure produced by it tend to increase at night. In CLARK'S (*l. c.*) experiments on roots severed from the tree, the rule was for root pressure to increase during the night and decrease during the day, for the whole period in which pressure was strong.

Taking the combined effect at night of increasing root absorption and decreased evaporation, there is a decided tendency toward an increase of pressure in the stem during the night. As the pressure increases the rate of infiltration also increases, tending thus to diminish the rate of increase of pressure (*fig. 3*). After sunrise evaporation begins to oppose the rise of pressure, so that about noon pressure begins to decline. The decreasing activity of the roots at this time aids the decline. What pressure might be developed in a birch stem by the prolonged action of root pressure, if the modifying influences of evaporation and infiltration could be eliminated, is shown by CLARK'S record of $193^{cm}$ pressure in a birch root severed from the stem. This pressure is more than double the pressures usually observed in the trunk.

Assuming that root pressure is essentially osmotic, the concentration of the sap in the root CLARK observed must have been about two and a half times that of the sap at the bases of trees I have observed. At different times during the sap season, I have evaporated sap from birches and found it to contain 0.5 to 1 per cent. of solids, largely

[4] MACDOUGAL, D. T., Soil temperatures and vegetation. Monthly Weather Review **31**:no. 8. 1903.

glucose. A sap containing 0.8 per cent. of glucose represents an osmotic pressure of about $78^{cm}$ at 0° C. It follows, then, that $100^{cm}$ of pressure in a birch stem is the maximum to be expected from root pressure.

*Volume changes in the sap and wood due to changes of temperature in the tree cause marked variations in pressure.*

I find that the expansion of sap from 6° to 32° C. is only 2 per cent. greater than the expansion of water. Cell wall substance, on the other hand, when saturated with water, expands about 2.2 times as much as water between 6° and 32° C. (*exp. 3*).

Observations as to the elasticity to the transmission of light of birch wood tissue in a thin microscopic section shows that wood fibers and the walls of the vessels in the wood have the least elasticity parallel to the length of the stem, and that the medullary rays have least elasticity along radii of the stem. In a wood fiber the greatest elasticity is perpendicular to the surface. By comparison with other substances, in which expansion by heat is directly related to elasticity to light, a different coefficient of thermal expansion for different directions would be expected in both single wood fibers and in masses of wood. My determinations made on strips of green white birch wood about $500^{cm}$ long immersed in water show that between 6° and 32° C. there is contraction instead of expansion in a radial direction when the temperature is raised. Under like conditions a longitudinal strip showed at first a slight expansion, but in two subsequent determinations it contracted. The coefficients of radial contraction obtained were 0.000005, 0.000004, and 0.000006; and those of longitudinal contraction were 0.000002 and 0.000003. These coefficients are so extremely small that they may be neglected in the following sap pressure calculations.[5] It thus appears that the volume changes in the cell walls above mentioned are made possible only by a diminution of the area of cross-section of the vessels and of the cavities in the cells, for the external dimensions of the tree change scarcely at all.

The effect of this tendency to diminish the pore space in the wood

[5] The thermal expansion—based upon *exp. 3* and upon the above coefficients—of a given volume of birch wood, of which 40–45 per cent. is saturated cell wall, amounts to about 1.5 times the expansion of an equal volume of water.

is to produce pressure on the liquid or gas occupying the pores. If liquid alone completely filled the cavities of the wood, any amount of thermal expansion would necessarily be accompanied by an equal amount of elastic expansion of the wood. Pressure in this case might be very great. It should be noted, however, that the pressure recorded by a gauge would be less than that developed in the tree without the attached gauge, for the sap forced from the tree into the gauge would partly relieve the pressure within the tree. It follows that the less the amount of sap required to operate a pressure gauge, the higher the pressure it will record for a given amount of thermal expansion within the tree.

It probably never happens that the wood of a birch tree becomes completely saturated with water. One or two per cent., at least, of gas is present in the wood fibers when the wood is densest. A smaller amount is present in the vessels. The compressibility of this gas lessens the effect of thermal expansion in producing pressure.

In order to obtain a quantitative statement of the amount of thermal expansion, I have made the following estimates. The small white birch ($11^{cm}$ diameter) of *exp. 1* has about 10 per cent. of its volume in small branches and twigs. These must vary in temperature in the same way that a blackened-bulb thermometer would, only in a less degree—say a maximum daily range of 20° C. The trunk would vary less in temperature than the air—say 10° C. The maximum daily change of volume of the sap and cell walls of the tree computed on this basis would be $270^{cc}$, or nearly 0.5 per cent. of the volume of the tree. Under such conditions the presence of as little as 1 per cent. of gas in the vessels would prevent an existing small pressure from rising more than about $40^{cm}$. The slight increase of pressure due to the greater expansive force of the gas at the higher temperature is so small that it may be disregarded.

We may now consider in detail some of the instances in which temperature controls pressure by causing volume changes within the tree. *Fig. 2* is a record of pressure, and of temperature as given by a blackened-bulb thermometer. The periods of lower temperature were caused by the passing of clouds. Pressure increased during the periods of sunshine and diminished during the intervals of shadow. From 3:00 to 3:20, while the sun shone bright, the temperature of the

thermometer increased 7° C. The corresponding increase in pressure was $30^{cm}$. It is impossible that any part of the tree except the smallest twigs could have been heated during so short a time more than 3 or 4°. There must have been, therefore, little or no gas in the vessels of the tree.

On April 21, 1906, from 2:00 to 2:45 P. M. (*fig. 3*), a rise of temperature of 4°.5 C. was accompanied by an increase of pressure of $20^{cm}$.

At sunrise on each of the mornings included in *fig. 3* the pressure curves steepen greatly.

During the afternoon of April 23, 1906 (curve *B*, *fig. 3*), the pressure was rising slowly till nearly sunset in response to a change of the weather with rising temperature.

From the foregoing discussions it may be reasonably inferred that there are two chief pressure-producing agencies concerned in the phenomenon of sap pressure in the birch stem, namely root pressure and thermal expansion. The effects of both are modified considerably by evaporation and by infiltration of sap into the wood cells. Root pressure and evaporation produce a daily oscillation of pressure, with the maximum shortly after sunrise and the minimum at sunset. Thermal volume changes in the tree cause a rise of pressure from sunrise till shortly after midday, and a fall from then till sunrise. Irregular minor oscillations of short period are caused by corresponding changes in air temperature or brightness of sunshine. The combined effect of the two agencies is to make the observed maximum come about midday and the minimum at sunset. The maximum is somewhat higher than would be produced by root pressure alone—in extreme cases twice as high.

If a tree is tapped when the pressure is high, the flow of sap is at first copious, but the rate of flow lessens rapidly. The pressure, as measured anywhere in the trunk, also declines (see *exp. 2* and *fig. 5*). The relation of pressure to flow during this period of falling is different for different relative positions of the gauge and the flowing orifice. Taking a theoretical case, the pressure as distributed over a radial section of a tree before tapping is represented in *A*, *fig. 4*. Lines of equal pressure are horizontal, and pressure increases downward. Shortly after tapping at *a*, the lines of equal pressure are as shown in *B*. A little later they are as in *C*. (The diagrams are constructed

for a case in which the resistance to flow of sap is twice as great radially as longitudinally.)

Now let the rate of flow for the first ten minutes after tapping be represented by *fig. 4, D*, curve *N*, and let *B* show the distribution of pressure at the end of two minutes, and *C* at the end of the 10 minutes. Let the pressure be measured at the three points *x, y, z*. The pressure in *x* before tapping is $40.5^{cm}$, at the end of 2 minutes it is $35^{cm}$, and at the end of 10 minutes it is $25^{cm}$. These values are plotted in *fig. 4, D*, curve *X*. The values for the pressure in holes *y* and *z* are likewise plotted in *fig. 4, D*, curves *Y* and *Z*. Inspection of these

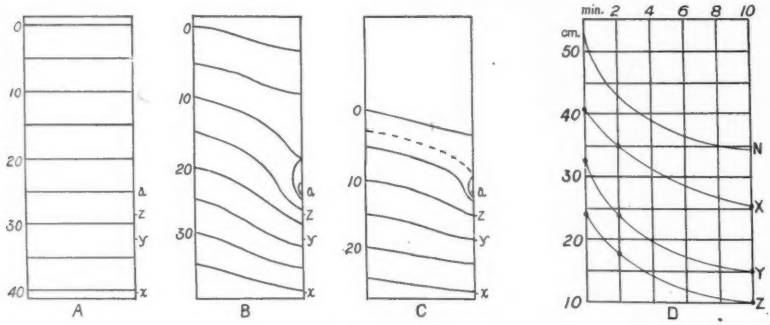



FIG. 4.—For explanation see text.

curves of pressure and the curve of flow shows that there is no definite general relation between pressure and flow.

## Experiments

EXPERIMENT 1.—During the evening of April 14, 1906, while the normal evening rise of pressure was in progress, a white birch (*Betula populifolia*) $11^{cm}$ in diameter and $6^{m}$ high was tapped for two gauges $157^{cm}$ vertically apart. The pressure from the first was more than enough to sustain a column of water as high as the tree. The difference in pressure of the two gauges was 12 to $12.3^{cm}$ of mercury, the hydrostatic pressure corresponding to this difference in the height of the two gauges being $11.6^{cm}$. This hydrostatic equilibrium may be explained on the supposition that a practically continuous column of water could have been traced through at least some of the ducts between the tap holes. Other ducts might have contained bubbles

of gas. That there was a small amount of gas present was shown by pouring mercury into the free arm of the lower gauge and thereby forcing back into the tree $0.45^{cc}$ of sap. This procedure caused the pressure within the tree to go up from 54 to $55.3^{cm}$. A simple calculation shows that there was a contraction of nearly 1 per cent. in the gas in the vessels. The total volume of gas contracting was then $45^{cc}$.

To get an estimate of the amount of duct space in the tree, I examined several cross-sections of branches about $2.5^{cm}$ in diameter. An area of $1.25^{sq\ mm}$ contained an average of 74 ducts, with an average cross-section of $0.002^{sq\ mm}$. The ducts, therefore, occupy about 12 per cent. of the volume of the tree. The volume of the tree (estimating the upper $3^{m}$ of the stem and branches as equal to the lower $3^{m}$ of the trunk) was $57{,}000^{cc}$. The duct space, then, amounted to about $6800^{cc}$. Finally, $45^{cc}$ (the gas content of the ducts) is nearly 0.7 per cent. of the volume of the ducts. A second addition of mercury gave the gas content as 1.3 per cent. The ducts, therefore, at this time of the year were almost entirely filled with water. In a larger tree, in which there is a good deal of heart wood, there might be considerably more gas in the ducts, but many of the ducts in the heart wood are probably not freely communicating with the ducts in the sap wood.

It was noticed in connection with adding the mercury to the gauge, that after the rise of pressure thus produced had taken place, the pressure remained stationary for 15 minutes the first time, and for 30 minutes the second time, and then began rising at its previous rate. Furthermore, the length of time that pressure was stationary was such that during that time pressure would have increased naturally the same amount that it was artificially raised. We may conclude from this that the *intensity* of root pressure was increasing during the night. This is in accord with the idea that the concentration of the sap in the roots—and the corresponding osmotic pressure—becomes greater when evaporation from the branches lessens.

EXPERIMENT 2.—Before sunrise April 16, 1906, when pressure was high and slowly rising, three holes were bored in a small birch trunk, about $1.5^{m}$ apart vertically. Gauges were attached to the lower holes and the upper one was plugged. Equilibrium was soon established between the gauges, the upper one reading $61.9^{cm}$ and the

lower one 76.3$^{cm}$. The difference (14.4$^{cm}$) is 2.8$^{cm}$ more than the pressure of the sap column between the holes. This is the condition that would obtain if sap were being artificially pumped into the base of the stem and were evaporating slowly from the top. Friction of the sap in the ducts would cause the lower gauge to read higher than if no current were flowing.

The gauge in the middle hole was then removed and the sap allowed to flow from the hole. A few minutes later the upper hole was unstopped, but no sap flowed from it, though sap had flowed from it when the hole was made. The flowing of the hole below it had caused it to cease to flow. As soon as the middle hole began flowing, the pressure in the lower hole dropped rapidly to 23.4$^{cm}$, and there remained nearly stationary for over an hour. The total drop in pressure in the lower hole was thus 52.9$^{cm}$, but in the hole above the drop was 61.9$^{cm}$. In other words, the pressure in the lower hole was 11.8$^{cm}$ more than enough to raise sap to the level of the flowing hole. This, also, is a condition to be expected if a current of sap was flowing upward from the roots through the stem, overcoming friction.

The flow from the middle hole was at first rapid—17 drops in 10 seconds—but it decreased in a few minutes to 8 drops per 10 seconds, and at the end of 20 minutes to 4 drops. The flow then continued at nearly this rate for more than an hour. Curves *A* and *B*, *D* and *E*, of *fig. 5* are plotted from these observations. Curve *C* shows the drop of pressure from a similar experiment on another tree. Although the curves are nearly parallel, the ratio of flow to pressure is greater for the highest pressure than for the lowest. This relation may be explained by assuming that the copious flow of the first few minutes had a double source of supply; the larger part came from the trunk, being forced toward the tap hole by the elastic expansion of the wood and the gas in the wood; and the smaller part came as a current from the roots. As soon as the excess of pressure in the stem had been relieved, the further and nearly uniform flow was kept up by the root pressure. Changes in the degree of cloudiness produced the waviness of the curves *C*, *D*, and *E* in *fig. 5*.

During the 20 minutes that the flow was decreasing 790 drops (66$^{cc}$) of sap escaped. Of this not more than 40$^{cc}$ or less than 25$^{cc}$ could have come from the roots. (This will be seen by a study of

curve *B*.) Therefore, 32$^{cc}$ is close to the amount supplied by the roots and therefore about 34$^{cc}$ came from expansion within the tree. The experiment of two days before showed the amount of gas in this tree to be 45 to 80$^{cc}$, an amount which, by expansion, is sufficient to account for the flow here considered.

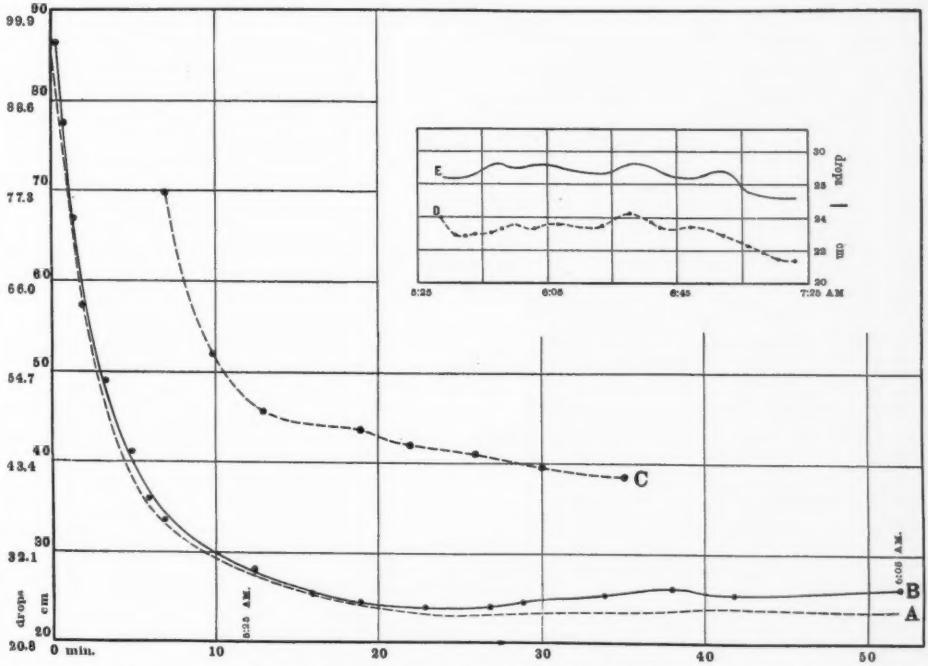



FIG. 5.—*A*, pressure at the base of a white birch, April 16, 1906, while flow was taking place from a hole higher up; *B*, rate of flow in drops per minute of the hole above *A;* the continuation of curves *A* and *B* are *D* and *E;* in another tree the decline of pressure while sap was flowing freely is shown by *C*.

EXPERIMENT 3.—To determine the amount of expansion of saturated cell-wall substance of birch wood.

Across the grain of a white birch plank thin shavings were taken. From these the air was entirely expelled under the receiver of an air pump. The shavings were then transferred to a 100$^{cc}$ pycnometer. The pycnometer was filled up with freshly boiled, distilled water, and weighed at 6° C., and again at 32° C. The weight of the pycnometer

full of water alone was also taken at these temperatures. Finally the weight of the completely dried shavings was found. Now the specific gravity of dry cell wall substance is approximately 1.56, and the volume of saturated cell wall substance is nearly 3/2 that of dry cell wall substance.[6] Then let $a$ = increase in weight of pycnometer full of water from 32° C. to 6° C.; $b$ = increase in weight of pycnometer full of water and shavings from 32° C. to 6° C.; $c$ = increase in volume of pycnometer from 32° C. to 6° C.; $d$ = volume of pycnometer; $e$ = volume of saturated cell wall substance; 0.0046 = expansion of $1^{cc}$ of water from 6° C. to 32° C. Then

$$\frac{b+c-(d-e)\left(\frac{a+c}{d}\right)}{e\times 0.0046}$$

= the ratio of expansion of cell wall to the expansion of water from 6° C. to 32° C.[7] Now, by substituting the values obtained in the experiment,

$$\frac{0.4975+0.066-(100-12.6)\left(\frac{0.433+0.066}{100}\right)}{12.6\times 0.0046}=2.2$$

= the desired ratio of expansion.

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[6] These are the figures given by SACHS, HARTIG, and others, and used in compiling the tables of the Vermont *Bulletin*.

[7] This formula would need slight corrections for more exact work, but it is more accurate than the factors of specific gravity and volume of saturated cell wall.

# BRIEFER ARTICLES

## CONCAVITY OF LEAVES AND ILLUMINATION

(WITH ONE FIGURE)

Concavity of the upper surfaces of leaves is of extremely common occurrence among the higher plants. WIESNER, in an important paper,[1] has discussed this concave upper leaf surface as a characteristic of the peripheral leaves of woody plants, and states that the leaves within the shadow of the crown of trees (with concave outer leaves) are generally flat or nearly so. He classes these and other leaves which are capable of

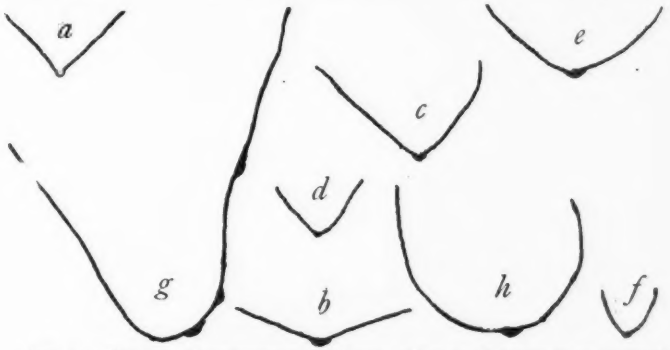


FIG. 1.—Diagram of cross-sections of leaves, taken at right angles to the midrib (if there is any) and through its middle point. ×⅓. *a*, Astilbe decandra; *b*, Prunus persica; *c*, Syringa vulgaris; *d*, Akebia quinata; *e*, Citrus medica; *f*, Styrax japonica; *g*, Begonia semperflorens; *h*, Schizophragma hydrangeoides.

some kind of temporary or permanent adjustment to the amount of light received as panphotometric leaves, regarding the concavity as useful in preventing injury to chlorophyll by excessive sunlight. OLTMANNS[2] calls attention to the fact that the leaflets of *Robinia Pseudo-Acacia* are concave on the south sides of trees, but flat on the north sides.

It seemed to the writer worth while to make some notes as to the occurrence of the concavity in question among various genera, particularly among trees and shrubs, and to take a few measurements of the amount of con-

[1] WIESNER, J., Anpassung des Laubblattes an die Lichtstärke. Biol. Centralbl. 1–15. 1899.

[2] OLTMANNS, F., Photometrische Bewegungen der Pflanzen. Flora 79: 232, 233. 1892.

cavity in shaded and unshaded leaves of the same individual. Most of the species observed were growing in the Botanic Garden of Harvard University. No attempt was made to pick out particular families for examination, but notes were made on any leaves, especially of dicotyledonous trees or shrubs, that showed decided concavity of the upper surface. Some slight amount of deviation from flatness seemed almost universal. The observations were made on mature vigorous leaves during the first week in September.

The leaves or leaflets examined in many instances showed a rather definite dihedral angle, as in *a* and *b*, *fig. 1*. More often the surfaces on each side of the midrib were decidedly curved, as in the cases *c–f*, while some leaves, as in *g* and *h*, showed no semblance of an angle in the cross-section, but formed a rather deep trough, with curved sides.

Measurements of angles were made by means of two straight-edged pieces of brass, hinged at one end and applied outside the leaf or leaflet at right angles to the midrib. In case the leaf surfaces were somewhat convex beneath, the angle taken was that subtended by a tangent to the middle points of the halves of the leaf.

Plants of 31 families of dicotyledons, comprising 52 genera and possibly 200 species, were noted as showing decided concavity of the upper surfaces of the leaves. Little attempt was made to find out how generally marked leaf-concavity characterized the various species of the genera examined. In some instances, e. g., Viburnum, it occurred in almost all the species accessible for observation, while in other cases, e. g., Magnolia, Acer, it was present in some species and absent in others.

The following measurements of dihedral leaf angles or concavities were obtained:

| Species | Angle in degrees, sunlight | Angle in degrees, shade |
|---|---|---|
| Akebia quinata (leaflets) | 106 | 167–180* |
| Magnolia acuminata | 80–180 | 180 or recurved |
| Astilbe decandra (leaflets) | 80–153 | 180 or recurved (167) |
| Hydrangea quercifolia | 134–180 | 180 or less |
| Schizophragma hydrangeoides | 28–180 | 180 or less |
| Fothergilla Gardeni | 80–180 | 180 or less |
| Robinia Pseudo-Acacia (leaflets) | 90–137 | 180* |
| Begonia semperflorens | 23–56 | 108–180 |
| Aralia pentaphylla (leaflets) | often semicircular | 180 |
| Ligustrum Ibota | 54–145 | 180 |
| Syringa vulgaris | 55–145 | 130–180 |
| Cephalanthus occidentalis | 102–153 | 180 |
| Viburnum nudum | 83–105 | 180 |

* The shade leaves were all measured from the densest shade afforded by the foliage of the plant itself. In the two cases marked by an asterisk the leaves were also in the shade of other trees or a wall.

It is undoubtedly a fact that the great majority of woody dicotyledons have leaves which when freely exposed to the sun are concave on the upper surface and that this concavity usually lessens or disappears in the case of much-shaded leaves on the same plant. WIESNER'S conclusion that this conformation is due to the effects of powerful illumination seems on the whole to be plausible. It is not safe, however, to assume, as he does, that we have here an undoubted case of protective adaptation, to ward off the injurious effect upon chlorophyll of excessive insolation. In order to prove this it would be necessary to explain many real or apparent exceptions to the assumption that greater concavity should go with greater illumination. To cite the first instances that occur: *Acer Negundo* is hardly, if at all, more exposed to excessive sunlight in its usual habitats than is *A. saccharinum*, and yet the former has trough-like leaflets, while the leaves of the latter are nearly flat. The Japanese *Ligustrum Ibota* comes from a region not enough more subject to excessive sunlight than that of the European *L. vulgare* to account for the great difference in the flatness of the leaves of the two species. *Vinca rosea*, a West Indian weed, might be expected to have leaves much more concave than those of the European *V. minor*, but the reverse is actually the case. Occasionally leaves growing in shade may be decidedly more concave than those growing under greater illumination, as I have noted in one case of *Kalmia angustifolia*. Finally, it is difficult to explain on any theory of utility of concave leaf surfaces in protecting chlorophyll the fact that the angular values obtained for leaves of the same individual, grown under similar conditions, vary so much. The angles given in the preceding table for each species were in many instances obtained from leaves which apparently received almost identical illumination, since they grew fairly near together and were sometimes almost in contact with each other. Yet, as will be observed, the angles for sun leaves sometimes varied in a ratio as high as six to one. Equally difficult to explain is the fact that in some genera, e. g., Prunus, Pyrus, Salix, the whole tree may show little difference in the flatness of the leaves, all being angled whether they grow in sun or shade.

Instead of trying, as WIESNER has done, to establish the critical intensity of illumination at which leaves of a given species cease to be panphotometric and become euphotometric, it would seem to the writer better worth while to look for some relation (always on the same individual) between illumination and the average amount of angular divergence of the halves of the leaf, basing all statements on a large number of measurements.—JOSEPH Y. BERGEN, *Cambridge, Mass.*

## ROEZL AND THE TYPE OF WASHINGTONIA

The palms on which WENDLAND founded his genus Washingtonia were grown from seed procured by ROEZL. They purported to have come from "Nord Mexico, bei Arizona, am Rio Colorado," but where they really came from has never been ascertained. In investigating the history of the genus it proved very difficult to obtain any account of ROEZL's American explorations. I was able to learn only of a journey made by him across the northern continent in 1872, and was therefore led to assert[3] that this was his only visit to our country. In fact, however, he had made a far more extended tour in 1868–1870, in the course of which he explored much of the United States and Mexico, and of Columbia in the southern continent. Some account of these journeyings is given in notes published by ORTGIES in volumes 20 and 23 of *Gartenflora*. Dr. TRELEASE, director of the Missouri Botanical Garden, has obligingly furnished me with an abstract of these notes, and from them I am able to present the following account of ROEZL's explorations in the United States.

ROEZL must have gone from Europe directly to Mexico, and he spent the winter of 1868–1869 in collecting in that state and in Yucatan. In March of the latter year he sailed from Havana for New York. He then visited several of the seaboard cities and made some collections in the Allegheny mountains, after which he departed for the west by way of St. Louis, Chicago, and Omaha. On July 15, 1869, he was in Cheyenne, and on August 28 in Truckee. Considerable time was devoted to collecting in Utah and Nevada, but by November 7 he had reached San Francisco, by way of Sacramento. After a run back to Nevada City he returned to San Francisco, and went thence to San Diego. The object of his southern trip was to gather *Delphinium cardinale*, and he sent to Europe two thousand roots that he supposed to be of that species. Eventually, on flowering they proved to be one of the blue larkspurs, probably *D. Parryi*. Here also he got two plants which were introduced to European cultivation as *Yucca schidigera* and *Y. Ortgiesiana*, unquestionably the species now known as *Yucca mohavensis* and *Hesperoyucca Whipplei*.

ROEZL returned to San Francisco in time to sail on January 18, 1870, for Panama, and after making extensive collections in Columbia and Mexico, again reached San Francisco August 1, 1870.

After a week spent in Hoopa Valley, he sailed for the north, visiting

[3] BOT. GAZETTE **44**:414. 1907. Footnote 10 on this page should be corrected as follows: *dele* **1839**:330; for Jour. Bot. **1874**: read **1834**:; for Gard. Chron. **2**:521. 1889 read Gard. Chron. N. S. **24**:521. 1888.

Astoria, Portland, and Ft. Vancouver. In September he was among the mountains of the upper Columbia River, but by October he had returned to the Sierra Nevada of California. It does not appear when he finally left California, but by the middle of December 1870 he was again in Panama. The first two months of the new year were devoted to revisiting Columbia, after which ROEZL returned to Europe.

It appears from this account that the only opportunity which ROEZL had of procuring seeds of Washingtonia was during his visit to San Diego, in December 1869. The notes, however, contain no reference to this palm. But a visit to any of its desert habitats would certainly have been an experience too notable to have failed of record. Nor is it probable that his visit to San Diego, so short and so diligently occupied in collecting, could have afforded time for the difficult journey to the desert. The vague and confused habitat assigned to the palm is itself a sufficient evidence that the collector, from whom the information must have come, could never have visited a native grove. It is safe to conclude that the seed he sent to Europe came from some of the older cultivated trees at San Diego, and that his pardonable ignorance of local geography prevented him from correctly understanding what was told him of the location of the indigenous groves. —S. B. PARISH, *San Bernardino, Cal.*

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## LONGEVITY OF SEEDS

In the BOTANICAL GAZETTE for January 1909, p. 69, CROCKER, in referring to my paper on this subject, concludes with the remark: "I believe I am doing the author no injustice when I say that it is impossible to tell from his paper in how far it is a contribution and in how far a compilation." May I say that the utmost care was taken to quote the authority for every record or fact that was not original, and that I am unable to find a single case in which this was not done. If any such omission occurs it is a purely accidental one, and I am prepared to offer both a public and a private apology to any author whose name is omitted as the authority for a record for which he is responsible. Naturally, however, if on repeating a test or experiment a more or less divergent result is obtained, the original authority can hardly be given for the changed statement of fact, which in many cases directly negatives the original record. The latter, however, is given in all cases with the author's name appended, so that it is difficult to see any foundation for CROCKER'S criticism.—ALFRED J. EWART, *University of Melbourne.*

REJOINDER

In spite of EWART'S very energetic objection to my criticism of his paper, I maintain that the criticism is entirely justifiable. To escape personal bias I have asked several persons to read passages of EWART'S article and to say who contributed the data. In every case they decided that they were EWART'S, though this is not the case.

As an example, I cite the first part of the paragraph beginning at the foot of p. 197, dealing with *Plantago major*, *P. Rugelii*, *Thlaspi arvense*, and *Avena fatua*. The data are all given in my article,[4] but one would not know from EWART'S statement that this was their source. Again, in the paragraph beginning near the top of p. 192, EWART gives the arguments against FISCHER'S conception of the cause of delayed germination in the seeds of water plants as if based on his own work. All these arguments are given in another paper of mine,[5] issued five months before EWART'S. In the same paragraph, he says: "Since the above was written, CROCKER (BOT. GAZETTE 1907, 374) has shown, etc." One would have expected a writer who is so careful to give credit where it belongs to recast this paragraph after he discovered my article, so as to indicate proper priority. I mention these as two instances out of several that furnished the basis of my criticism.

EWART speaks again of his results contradicting mine in a number of cases. I must therefore point out again that the matters in dispute are minor details and not cardinal principles in the physiology of delayed germination; and I should be glad to have anyone compare his paper and my criticism to judge in how far there is evidence that his results disprove mine. I have repeated the experiments upon the disputed points, and have had various competent students do so independently. The results in every case agree with my previous conclusions, as my criticism points out.

I am sorry that what I considered and still consider a fair criticism has led to undue publicity. I am sure, however, that neither a public nor a private apology is necessary from EWART, as the case will rest upon its merits.—WILLIAM CROCKER, *The University of Chicago.*

[4] CROCKER, W., Rôle of seed coats in delayed germination. BOT. GAZETTE **42**: 282–284. 1906.

[5] ———, Germination of seeds of water plants. BOT. GAZETTE **44**: 375–380. 1907.

# CURRENT LITERATURE

## MINOR NOTICES

**Malayan ferns.**—This work[1] presents in a single volume a synoptical treatment of all ferns known to occur in the Malayan Archipelago; its elaboration has been carried on mainly at Buitenzorg, where the facilities for studying dried and living material of this group of plants are exceptionally good. A compendium of the families, tribes, and genera introduces the body of the work; and the sequence of families, the limitation of genera, and the nomenclature are for the most part in accordance with ENGLER and PRANTL'S *Natürlichen Pflanzenfamilien*. Fairly concise and clear keys precede the carefully drawn descriptions whenever the genus consists of two or more species, and the bibliography and synonomy are given in some detail; but it is unfortunate that the author has cited so few exsiccatae. The extended spacing and the numerous blank pages make the volume unnecessarily bulky. Moreover, the appendix of some 58 pages, treating principally of ferns discovered after January 1, 1907, and 11 pages of "additions, modifications, and corrections" which the author suggests "may be cut out and pasted on the places indicated" will mar materially the practical use of the work. It would seem almost as though publication might better have been delayed until such necessary additions and corrections could have been incorporated in the body of the text. On the whole, however, the work represents careful co'lation, combined with a large amount of original research, and presents in available and reliable form a comprehensive treatment of approximately 1500 species and numerous varieties, representing 10 families and 95 genera. The book doubtless w ll find a useful place in the taxonomic literature of ferns.—J. M. GREENMAN.

**Warming's *Ecology of plants*. A correction.**—My attention has been called to an unfortunate error in my review of WARMING'S *Ecology*,[2] viz., the statement that the work was written in English by the author, assisted by Dr. VAHL. As a matter of fact the work, as it has appeared, is a translation by Professors BALFOUR and GROOM from manuscript prepared by Professor WARMING and Dr. VAHL. My mistake was due to the statement on the title-page: "prepared for publication in English by PERCY GROOM," etc. (which might have been less vague if printed: "translated from manuscript," etc.), and by a personal knowledge of WARMING'S facility in the English language. It is certainly scant

[1] VAN ALDERWERELT VAN ROSENBURGH, C. R. W. K., Malayan ferns. Handbook to the determination of the ferns of the Malayan Islands (incl. those of the Malay Peninsula, the Philippines, and New Guinea). Royal 8vo. pp. xl + 899 + 11. Batavia: Landsdrukkerij. 1908.

[2] BOT. GAZETTE **48**: 149–152. 1909.

enough credit to a translator to acknowledge his full share in such a work as this, a share that is most burdensome, and too little appreciated as a rule. English and American readers are certainly most grateful to Professors BALFOUR and GROOM for making accessible not only this new ecological treatise, but the other great ecological masterpiece as well, SCHIMPER'S. *Plant geography*.—H. C. COWLES.

**Pharmakognostischer Atlas.**—KOCH[3] has followed his *Mikroskopische Analyse der Drogenpulver* with a second part for the use of apothecaries, wholesale druggists, sanitary officials, students of pharmacy, etc. In the arrangement of the text the author has followed his old scheme of different types, numerals, and indentations for greater facility in locating the various histological structures. Each drug has careful outlines on its preparation for microscopical observation and detailed descriptions of the individual tissues. Excellent plates of transverse and longitudinal sections serve to make these descriptions remarkably clear. The first *Lieferung* is devoted to cascarilla, red cinchona, and cinnamon barks. The complete work will certainly be useful in the recognition of crude drugs.—K. G. BARBER.

**Methods in microscopy.**—The second edition of the *Praktikum* of MÖBIUS[4] has about the same scope as the first. Directions are given for making preparations and also for some study of the preparations. Only the simplest methods are given, no attention being paid to the paraffin method or to critical methods of staining; in fact, most of the directions, in American schools, would be given orally or would be written on the blackboard for elementary classes which have no need as yet for any complicated technic. Of the 123 pages, 92 are devoted to spermatophytes, 6 to pteridophytes, 5 to bryophytes, and 20 to thallophytes. —CHARLES J. CHAMBERLAIN.

## NOTES FOR STUDENTS

**Genetics.**—In the fourth report to the Evolution Committee of the Royal Society, BATESON, SAUNDERS, and PUNNETT[5] present an account of their further studies with poultry, sweet peas, and stocks. Valuable summaries are given of all the studies that have been made on these subjects, the most interesting feature being the further evidence of the occurrence of such ratios as 7:1:1:7 and 15:1:1:15. It is suggested that the types of gametic coupling evident in cases of this kind might explain the occurrence of certain aberrant forms which are generally looked upon as mutants. The term "spurious allelomorphism" is proposed

[3] KOCH, LUDWIG, Pharmakognostischer Atlas. I, Die Rinden. I Bd. 1 Lief. pp. 26. *pls.* 5. Leipzig: Gebrüder Borntraeger. 1909. *M* 3.50.

[4] MÖBIUS, MARTIN, Botanisch-mikroskopisches Praktikum für Anfänger. Second edition. 8vo. pp. ii + 123. Berlin: Gebrüder Borntraeger. 1909. *M* 3.20.

[5] BATESON, W., SAUNDERS, MISS E. R., AND PUNNETT, R. C., Experimental studies in the physiology of heredity. Reports to the Evolution Committee of the Royal Society 4: 1–40. 1908.

for the phenomenon of repulsion between two dominant factors or units, as for example when blueness and the erect standard in peas cannot be combined in the same individual, but are found to repel one another. The further work with stocks has mainly had reference to the phenomenon of doubling. The doubled stocks are always completely sterile and cannot be used for breeding purposes, so that it is not easy to determine the significance of this phenomenon. It is found that single stocks are of two kinds, one of which breeds true to the single, the other of which always throws a certain proportion of doubles when mated with its own kind, and the conclusion is drawn that this second type of single stock is perhaps a heterozygote in which the single character is dominant to the double. In stocks a difference is also found in the constitution of the pollen grains and ovules on the same plant. The presence and absence hypothesis is definitely accepted, and Miss DURHAM[6] in another paper appended to the report shows that on the basis of "presence and absence," the difficulties which CUÉNOT had found in certain mouse crosses completely disappear.

In a discussion of the "presence and absence" hypothesis the reviewer[7] has shown that the absence of a character may be dominant over its presence quite as well as the reverse. A simple experiment to illustrate this among the other salient features of Mendelian inheritance has also been described.[8]

He has also published the results[9] of his investigation into the elementary species and hybrids of *Bursa Bursa-pastoris* and *B. Heegeri*, showing that the leaf characters of four elementary forms which were found in nature behave in the typical Mendelian fashion on crossing with one another. The same relation is found to exist between *B. Bursa-pastoris* and *B. Heegeri* that exists among the several elementary components of the former species, thus giving new proof of the derivation of the latter species from the former. However, the *Heegeri* type of capsule which disappears in the first generation of the hybrids reappears in the second generation in a ratio of about 22:1. The important feature of these results for evolution is the fact that four pure-breeding elementary species of *B. Heegeri* resulted from the cross, when only one had been found before.

CORRENS[10] has studied variegation and yellow-green foliage in Mirabilis, Urtica, and Lunaria, in which he shows that the yellow-green form, which he

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[6] DURHAM, FLORENCE H., A preliminary account of the inheritance of coat-color in mice. Reports to the Evolution Committee 4:41–63. 1908.

[7] SHULL, G. H., The "presence and absence" hypothesis. Amer. Nat. **43**:410–419. 1909.

[8] ———, A simple chemical device to illustrate Mendelian inheritance. Plant World **12**:145–153. 1909.

[9] ———, *Bursa Bursa-pastoris* and *Bursa Heegeri:* Biotypes and hybrids. Carnegie Institution of Washington, Publ. 112. pp. 57. *figs. 23. pls. 4.* 1909.

[10] CORRENS, C., Vererbungsversuche mit blass (gelb) grünen und buntblättrigen Sippen bei *Mirabilis Jalapa, Urtica pilulifera,* und *Lunaria annua.* Zeitschr. Abstam. Vererb. **1**:291–329. *figs. 2.* 1909.

calls *chlorina*, and the white-margined variety or *albo-marginata* are Mendelian in their hereditary behavior, both these forms being hypostatic to green and the *chlorina* hypostatic to *albo-marginata*. Two variegated varieties of *Mirabilis Jalapa*, on the other hand, give quite unexpected results. It appears that the offspring is more or less dependent upon the character of the particular branch upon which the seed was produced. BAUR[11] has found a similar behavior in the white variegated Pelargonium; thus the offspring of a pure white branch gives nothing but pure white seedlings which are incapable of successful growth, while the offspring of pure green branches produce only pure green seedlings. BAUR goes into the anatomy of the white-margined varieties, and shows that there is a complete chlorophylless sheath overlying the chlorophyll-bearing tissues, and extending beyond them at the margin. BAUR's theory for the production of such variegated varieties is that the yellow and chlorophyll-bearing plastids are distributed into the two daughter cells at each cell division, and by chance occasionally only nonchlorophyll-bearing plastids are included in one of the daughter cells. Thereafter this white cell gives rise to a cell progeny containing no chlorophyll and thus forming a white patch or streak which is the product of this one cell. When the division is anticlinal the variegation is in blotches, and when periclinal the white tissue becomes either median or marginal, only one case of the median type having been observed. BAUR'S results seem to indicate that the male germ cells, as well as the female, contribute characteristic plastids to individuals produced by their union, but this has not yet been actually observed.

The possibility that different parts of a plant may present different hereditary qualities, as shown by CORRENS and BAUR in these variegated varieties and as very generally recognized in the case of the relatively infrequent vegetative mutations known as bud-sports, is considered a matter of considerable importance by DE LOACH,[12] who seems to have found that in certain cotton hybrids some capsules of the heterozygote have the characters of the one or the other parent practically "fixed," while others give a large degree of splitting. Such suggestions as this open up interesting fields for investigation, but theoretically it does not seem likely that different parts of the same individual plant can *generally* have its own special type of heredity.

EMERSON[13] brings together the work that has been done in the study of Mendelian characters of beans, and finds that all evidence now at hand supports the reviewer's statement that in certain varieties of beans a unit character for mottling is present, which produces an external manifestation only when in the

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[11] BAUR, E., Das Wesen und die Erblichkeitsverhältnisse der "Varietates albo-marginatae Hort." von *Pelargonium zonale*. Zeitschr. Abstam. Vererb. **1**:330–351. *figs. 20*. 1909.

[12] DE LOACH, R. J. H., The Mendelian and DeVriesian laws applied to cotton breeding. Georgia Experiment Station, Bull. 83: 43–63. *figs. 7*. 1908.

[13] EMERSON, R. A., Factors for mottling in beans. Annual Report American Breeders' Association **5**:368–376. 1909.

heterozygous state. EMERSON concludes that there are two distinct and unrelated units for mottling, one of which is a typical Mendelian dominant, the other becoming evident only in the heterozygous state, and on this basis he works out the expectation of various types of crosses. It remains to be demonstrated by actual breeding that such peculiar ratios may exist as 11:5, 21:38, 33:15, 16, etc.

A number of more or less popular expositions of Mendelism have appeared, and it is not necessary to mention these except in case new scientific matter has been used by way of illustration. One of the best of these general discussions is that of BAUR,[14] in which the illustrative material is almost entirely derived from his own experiments with *Antirrhinum majus*. In this species 15 or more different hereditary units have been demonstrated, and the author inclines to the view that much of so-called fluctuating variation is really Mendelian splitting of less prominent unit characters. The number of demonstrated units in this species exceeds the number of chromosomes, which leads the author to the conclusion that whole chromosomes cannot be the units upon which these characters depend. BAUR adheres strictly to the presence and absence hypothesis. SPILLMAN,[15] in a review of BAUR's paper, shows that so far as yet demonstrated the individual chromosomes may be the fundamental bases of these unit characters, although several instances are known in which the number of demonstrated unit characters in a species is in excess of the known number of chromosomes. The crucial test must be the finding of an *individual* having more independent characters than it has chromosomes. This has not yet been done.

DARBISHIRE[16] has once again repeated one of MENDEL's original experiments in order to determine whether there is any influence of pre-parental ancestry upon the offspring, a question involving the essential difference between the Mendelian and Galtonian conceptions of heredity. It was well that this experiment should be undertaken by one who was in the beginning a staunch Galtonian. The result of the experiment leads DARBISHIRE to the conclusion that "there is nothing like ancestral contribution within the limits of a single unit character," or in other words that segregation is perfect and the recessive character appears in as large a proportion of the offspring of a heterozygote after six generations of selection to the dominant character as in the $F_2$.

The Mendelian theory of heredity has produced a very deep impress upon the practical work of plant and animal breeding, and a considerable number of papers have appeared from economic sources which present valuable additional data in support of this theory, and indicating the extent of its applicability. Only a few of the more important of these papers can be noted here. Besides the paper

[14] BAUR, E., Einige Ergebnisse der experimentellen Vererbungslehre. Beih. medizinischen Klinik **4**:265–292. 1908.

[15] SPILLMAN, W. J., The nature of "unit" characters. Amer. Nat. 43:243–248. 1909.

[16] DARBISHIRE, A. D., An experimental estimation of the theory of ancestral contributions in heredity. Proc. Roy. Soc. London B **81**:61–79. 1909.

of DE LOACH already mentioned, which shows that Mendelian behavior occurred in a certain cotton hybrid, BALLS[17] has discussed cotton hybrids in a comprehensive way, showing that at least 21 characteristics of the cotton plants behave as unit characters. BALLS declares that, while he does not know the exact number of chromosomes in the cotton nucleus, there are certainly not over 20, thus placing cotton with Pisum and Antirrhinum, as species in which the number of known unit characters exceeds the number of chromosomes. SUTTON[18] has carried on extensive crossings in Brassica and found that in a cross between the Swede turnip and the Ragged Jack kale there is a strict Mendelian behavior in which two unit characters are involved, namely, the fleshy character of the root and the curled leaves. The ratio of 9:3:3:1 appeared very clearly in the reciprocal hybrids of the cross. The glabrous-leaved brassicas (*B. oleracea* and its allies) would not cross with the hispid-leaved species (*B. rapa*, *B. campestris*, etc.), and crosses between the turnip and Swede turnip were sterile.

NILSSON-EHLE[19] maintains that practically all of the supposed mutants if not all which have been found in wheat, oats, and other similar grains split after the Mendelian fashion, and are in reality the results of occasional cross-fertilizations, i. e., of "vicinism." The most important result reported by NILSSON-EHLE is the finding of several instances in wheat and oats, in which apparently identical external characters are produced by the presence of two or more independent units, thus resulting in the $F_2$ ratios 15:1, 63:1, and perhaps 255:1 (observed ratio 274:1). In following generations some plants from crosses which showed 15:1 in $F_2$ give ratios of 3:1, and others again 15:1. In a red-grained × white-grained wheat, which presented the ratio of 63:1 in $F_2$, some plants in $F_3$ gave again the ratio of 63:1, some 15:1, and some 3:1, thus confirming the author's conclusion as to the manner in which the ratios 15:1 and 63:1 arise, and showing them to be typically Mendelian. The ligula of oats was absent in only one variety used in the experiments. This crossed with numerous other varieties gave ratios 3:1, 15:1, 63:1, and in one case apparently 255:1 (actually 274:1), in different crosses. He concludes that his results prove the correctness of the presence and absence hypothesis, and that not a single fact among his crosses is opposed to the "purity" of the gametes. He also, like BAUR, would explain the inheritance of certain apparently fluctuating characters as due to Mendelian splitting of units having similar functions.

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[17] BALLS, L., Some cytological aspects of cotton breeding. Ann. Rep. Amer. Breeders' Assoc. **5**:16–28. 1909.

[18] SUTTON, ARTHUR W., Brassica crosses. Jour. Linn. Soc. Bot. **38**:338–349. *pls. 12*. 1909.

[19] NILSSON-EHLE, H., Einige Ergebnisse von Kreuzungen bei Hafer und Weizen. Botaniska Notiser 257–294. 1908.

———, Kreuzungsuntersuchungen an Hafer und Weizen. pp. 122. 1909. Lund: Hakan Ohlssons Buchdruckerei.

EAST[20] finds that dent and flint corns differ from one another in a considerable series of correlated characters, and that these combinations of characters are maintained when these types are bred with the sugar corns. Although the flint or starch character of the grains is not then visible, breeding tests show that one or the other of these is latent, so that there is a "flint" series of sugar corns and a "starch" series.

So far as evidence goes at the present time, the Mendelian method of behavior is most clearly present in crosses between the most nearly related forms, and shows the most decided tendency to break down in the crosses between more distantly related things. For this reason all studies of the behavior of species-hybrids become of the greatest importance. HURST[21] has made a survey of orchid hybrids with special reference to the inheritance of albinism, and finds the phenomena so similar to those already worked out in sweet peas and stocks that he is convinced that they present typical Mendelian segregation. LOCK[22] gives a report on some species crosses of the genus Nicotiana. This is only a preliminary report and many points remain to be cleared up. He finds that the second generation of some of these crosses shows a wide range of distinct types, which he believes can be analyzed on the same basis as the sweet peas and stocks have been. Color of pollen and of corolla, and form of corolla tube (bulged or funnelform) showed typical segregation. In many characters pertaining to general habit, leaf form, etc., segregation was not present or only doubtfully. LOCK suggests the possibility that "true-breeding" hybrids may result from the failure of any but homozygous combinations, this idea being made possible by the fact that very often the fertility of such hybrids is very low, so that but a small percentage of successful seeds is produced. This matter of non-splitting hybrids between species has also been presented by BURBANK,[23] who points out that this presents a method of production of new species, probably more important than usually supposed. Although several of the instances mentioned by BURBANK have not been sufficiently tested, there can be little doubt that the species-hybrids in Rubus present cases of this kind. Upon these exceptional situations the chief attention of experimenters should be concentrated.

Another hopeful direction for research that is being taken up in several quarters is that of making analyses to determine the exact nature of the unit characters. Only in this way can we hope to discover the nature of the character-producing

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[20] EAST, E. M., A note on the inheritance in sweet corn. Science N. S. **29**:465–467. 1909.

[21] HURST, C. C., Inheritance of albinism in orchids. Gardeners' Chronicle. Feb. 6, 1909.

[22] LOCK, R. H., A preliminary survey of species crosses in the genus Nicotiana from the Mendelian standpoint. Ann. Roy. Bot. Gard. Peradeniya **4**:195–227. *pls. 12.* 1909.

[23] BURBANK, L., Another mode of species-forming. Ann. Rep. Amer. Breeders' Assoc. **5**:4–41. 1909; also, Pop. Sci. Monthly 264–266. Sept. 1909.

genes. There is a growing sentiment that all hereditary phenomena must rest in last analyses upon a chemical basis. DARBISHIRE[24] has made a careful examination of the starch grains of round and wrinkled peas in pure-bred strains and in several generations of their hybrids. He finds that there are several uncorrelated features of these starch grains which result in the hybrids having some of the characteristics of the starch grains of both the parents, thus tending to obscure the fact that the segregation of the starch characters is perfect.

Miss WHELDALE[25] has studied the floral pigments of a large number of species, devoting her attention most intently to the anthocyan series, but also including a discussion of xanthein, xanthin, and carotin. A useful summary is given of the studies of others upon the chemical composition of these compounds, and a large number of observations from her own analyses are presented, the general result being to show that there is a very large number of different pigments having a common fundamental structure which pass under each of these several names. From these analyses and from experience in cross-breeding she concludes that at least two features are necessary to the production of the anthocyan color: the one a colorless aromatic chromogen of the flavone series, the other an oxidizing agent which she believes to be a ferment. The details of Miss WHELDALE's methods of analysis and the lengthy list of literature will prove of great value to students who desire to go into these more intimate problems of genetics.

A similar work from the animal side has been attempted by RIDDLE,[26] with respect to the melanin compounds, though the author presents no work of his own, simply bringing together in an instructive way the more recent results of investigations in this field. One unfortunate feature of RIDDLE's work is his unfamiliarity with the Mendelian work from the experimental point of view. He thinks that he has proved the utter fallacy of the entire body of Mendelian teaching, and that he has demonstrated the continuity of the so-called unit characters, a statement which contravenes the experience of all investigators who have studied the behavior of pigment characters in actual breeding. No epigenetic hypothesis as yet gives the slightest hope of enabling such predictions as are successfully made continually by workers with the unit character conception.—GEORGE H. SHULL.

**Perception of light.**—HABERLANDT[27] attempts to strengthen his theory of light perception by plants, especially on the physiological side, acknowledging

[24] DARBISHIRE, A. D., On the result of crossing round with wrinkled peas, with especial reference to their starch grains. Proc. Roy. Soc. London B **80**: 122–135. 1908.

[25] WHELDALE, Miss M., The colors and pigments of flowers, with special reference to genetics. Proc. Roy. Soc. London B **81**: 44–60. 1909.

———, On the nature of anthocyanin. Proc. Cambridge Phil. Soc. **15**: 137–168. 1909.

[26] RIDDLE, O., Our knowledge of melanin color formation and its bearing on the Mendelian description of heredity. Biol. Bull. **16**: 316–351. 1909.

[27] HABERLANDT, G., Zur Physiologie der Lichtsinnesorgane der Laubblätter. Jahrb. Wiss. Bot. **46**: 377–417. 1909.

that the experimental work there leaves much to be desired, while the anatomical relations have been pretty fully cleared up. He discusses, therefore, the investigations that have attempted to eliminate the lens action of the papillose epidermis by making plane the surface with water, oil, gelatin, etc.; after which he addresses himself to the question of the residual lens action of the epidermal cells. He shows that in all cases with oblique illumination there remains an unequal excentric distribution of the brightness on the inner walls of the epidermal cells, though of less intensity than with dry epidermis. Inquiring into the sensitiveness of the cells in distinguishing differences of illumination, it appears that the more sensitive leaves have about the same capacity, 1/30, as the human eye under ordinary circumstances, the extremes being 1/75 and 1/12.5. But the differences of illumination in the case of papillose epidermis, even when wetted, is far above these figures, and, as HABERLANDT proceeds to show, is often greater even in leaves that have the epidermal cells plane outside and concave on the inner end. In the latter case the differences were from 1/15 to 10/1, according to the obliquity of the light.

After discussing the previous more or less contradictory results of the wetting method, in which some of the experimental leaves were not in condition to perceive the direction of the light and to respond to it, he describes his new method. This consists of wetting only a part of a leaf of Tropaeolum with water made plane with a thin sheet of mica, and leaving the rest dry. A zone between the wet and dry portions is darkened with a paper screen, and the petiole is also properly protected. Then the two regions are illuminated obliquely from contrary directions. By varying the relative areas of the wet and dry regions, and the intensity of the illumination, it is easy to determine the relative efficiency of the epidermis under the two conditions. When the areas are equal and the wet area receives double the intensity of light, its direction on the dry side controls the response. When the intensities are equal and the wet area is 2.2–4.8 times the dry, the latter still dominates the reaction.

We translate the latest statement of HABERLANDT'S theory: "The perception of the direction of light results, according to my theory, from the differences in brightness or the different distribution of intensity upon the inner walls of the epidermis, which may be brought about in various ways. The smaller differences of brightnesss may be produced by the mere convexity of the inner walls of the epidermis. These *must* suffice as a stimulus (*müssen die Reizschwelle erreichen*) if the outer walls are plane and concentration of the light is thus excluded; and they *may* suffice even if the normal collection of light by convex outer walls is made impossible by wetting. Then even the wet leaf perceives the direction of the light and returns, although slowly and generally incompletely, to the usual light position. In these cases the epidermal cells act as optical stimulators, and and though they may be dispensed with to a certain extent, the promptness and precision of the movement are enhanced by their effect in increasing the intensity of the stimulus. This action is especially valuable in the last phases of the adjustment, when by the diminution of the angle of incidence, the differences of bright-

ness on the inner walls, so far as these differences are due to the convexity of the inner walls, may become less and less until they fall below the liminal value as a stimulus."—C. R. B.

**Symbiosis in orchids.**—A recent paper by BERNARD[28] recalls his previous studies on the germination of certain orchid seeds and on the relation of fungi to the tuberization of orchids and potatoes. The present paper advances our knowledge of these fungi and places considerable emphasis upon their place in the development of the orchid group. Three species (*Rhizoctonia repens*, *R. lanuginosa*, and *R. mucoroides*) have been recognized, described, isolated, and grown in pure cultures for considerable periods. Although no spore-bearing structures have been observed, they probably belong to the lower basidiomycetes. The first-named species seems to be the most primitive and most widespread in its symbiosis.

Two series of orchids were studied, those of epiphytic and those of terrestrial habit. The growth of the seedlings was accomplished experimentally in test tubes upon suitable media, and the effect of the fungi and of various concentrations of the media upon their development carefully studied. The results are most interesting and suggestive, and may be summarized as follows: (1) Orchids exhibit a progressive development of symbiosis corresponding to and probably in some measure the cause of their development in phylogenetic series. (2) The evolution in epiphytic and terrestrial families is parallel, and symbiosis is the only common factor which can account for this parallelism. (3) The evolution in symbiosis manifests itself in an advance from independent germination of seeds with normally developed seedlings, to a germination entirely dependent upon the infection of the embryo by fungi and the development of seedlings characterized by protocorms. In the adult plants various progressive stages of symbiosis are exhibited, from an intermittent infection with sympodial habit to permanent symbiosis associated with the monopodial habit of the host. (4) The fungi vary in virulence according to their species, their host, and the length of time they have lived outside those hosts. Very virulent cultures act upon more highly developed orchids in a similar manner to more attenuated cultures upon more primitive species. (5) Concentrated solutions of the culture media have an effect upon germination similar to that produced by infection by fungi, and both symbiosis and growth in concentrated media result in increasing the concentration of the cell contents, which seems to be the necessary condition for the development of these specialized plants.—GEO. D. FULLER.

**Recent contributions from the Gray Herbarium.**[29]—A. EASTWOOD (Proc. Am. Acad. **44**:563–591. 1909) has published a "Synopsis of the Mexican and

[28] BERNARD, NOËL, L'évolution dans la symbiose. Les orchidées et leurs champignous commensaux. Ann. Sci. Nat. Bot. IX. **9**:1–196. 1909.

[29] Contributions from the Gray Herbarium of Harvard University, New Series, No. XXXVI (Proc. Am. Acad. **44**:563–637. 1909); and No. XXXVII (Proc. Bost. Soc. Nat. Hist. **34**:163–312. *pls. 23–30.* 1909).

Central American species of Castilleja" in which 54 species are recognized, 17 being new to science. A clear and concise key precedes the enumeration and description of species; the same author (*ibid.* 603–608) describes 12 new species of Mexican flowering plants belonging to different genera.—B. L. ROBINSON (*ibid.* 592–596) in a "Revision of the genus Rumfordia" records six known species, of which two are here described for the first time, and (*ibid.* 613–626) under the title "Diagnoses and transfers of tropical American phanerogams" publishes 20 new species and three new varieties, and makes several new combinations.—H. H. BARTLETT (*ibid.* 597–602) gives a "Synopsis of the American species of Litsea," recognizing 11 species, 5 of which are new, and (*ibid.* 609–612) under "Notes on Mexican and Central American alders" describes one new species and three new varieties; the same author (*ibid.*, 627–637) has published 14 new species and varieties of flowering plants chiefly from Mexico, and proposes one new genus (*Basistelma*) of the Asclepiadaceae.

J. R. JOHNSTON has recently issued, as Contribution no. 37 of the above series, a "Flora of the islands of Margarita and Coche, Venezuela," based chiefly on his own observations and collections made on the islands during two expeditions, one in 1901, the other in 1903. A brief historical sketch of the botany of the islands, an account of the physical features, a catalogue of the species, a list of the economic and medicinal plants, the distribution of species, the composition and relationship of the flora are the main topics presented, to which is added a bibliography of all works that relate directly to the vegetation of the islands. Approximately 650 species are known from Margarita and Coche at the present time; and the author estimates that this number represents about three-fourths of the entire flora. Forty-two species and two new genera have been discovered on Margarita during the course of Mr. JOHNSTON's preparation of the present publication. The relationship of the flora, as would be expected, is with the mainland. The work forms an excellent basis for future investigations on the flora of the islands; it is, moreover, of particular scientific value since the plants on which the catalogue of species is based are deposited in several of the larger herbaria of Europe and America.—J. M. GREENMAN.

**Anatomy of Zamia.**—MATTE[30] has recently published an addition to the number of investigations in the interesting field of cycad anatomy. Zamia is the subject of the present work, the species studied being *Zamia floridana* and *Z. integrifolia*. The paper shows the anatomy of Zamia to be of the ordinary cycad type.

In the embryo, the vascular plate of the cotyledonary node is a protostele. Each cotyledon receives three strands, which undergo the usual branching and anastomosing, and exhibit transfusion tissue at the tips. At the base of the cotyledons the strands are mesarch and may be even concentric; they are exarch in the middle and upper regions. The first leaves are opposite, but later ones

[30] MATTE, H., Sur la structure de l'embryon et des germinations du genre Zamia L. Bull. Soc. Sci. et Med. de l'Ouest **18**: nos. 2 and 3. 1909.

have the spiral arrangement. The leaf traces arise in the cortex, between the cotyledonary bundles, and there are three for each leaf. Girdling is acquired early. There is no clearly differentiated root structure in the embryo.

The manner of germinating is the same as that described for other cycads. The tardily appearing root is tuberized by the activity of a zone of cambium which appears immediately within the endodermis, and proliferates to such an extent that the components of the root cylinder are displaced and the cortex is exfoliated. The root cylinder may be diarch, triarch, or tetrarch, and reduces toward the tip. In its lower part all the tissues are well differentiated, even the endodermis and pericycle. The stems of young seedlings have no secondary wood, the cylinder being composed entirely of endarch leaf traces, which become mesarch farther out in the leaf. The pith of this siphonostelic stem sometimes contains a few isolated vessels. Contrary to the usual custom of looking upon these vessels as remnants of the embryonal protostele, the author prefers to regard them as vestiges of ancestral structure.

MATTE corroborates the discoveries made by LAND and the reviewer that the cotyledonary node of Zamia is of the usual cycad type, that there is a tendency to lobing at the tips of some of the cotyledons, and that there is an irregularly arranged cortical cambium, though he describes the last as vaguely cambiform, and does not attribute to it any phylogenetic significance.

The microphotographs are a retrogression from the clear and beautiful drawings of the earlier papers.—HELEN A. DORETY.

**Temporary anaerobiosis.**—NABOKICH has published from time to time in the past ten years short papers upon the behavior of plants under anaerobic conditions; now he gives us a monograph on the temporary anaerobiosis of higher plants.[3] There is an elaborate consideration (45 pp.) of the previous work, practically all of which is decidedly adverse to his views. Then follows the experimental part, showing how anaerobic growth is recognizable and presenting the results of an analysis of its physiological characteristics, its periodicity, dependence on temperature, rôle of sugar and alcohol, energetics, and cell division.

NABOKICH reports two categories of physiological facts which are not clearly consonant. On the one hand, anaerobic growth seems to be identical with aerobic as to the grand period, geotropic response, and cell division (including karyokinesis). On the other hand, there are peculiarities of anaerobic growth, such as the course of its curve at different periods (though this can be paralleled in aerobic growth under proper conditions), its specific dependence upon temperature and sugar solutions, and the invariable death of the cells. Though NABOKICH holds that his experiments have fully established his fundamental assumption of the capacity of higher plants for anaerobic growth, he confesses that he has not succeeded in obtaining an amount of growth beyond the limits of possible for-

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[3] NABOKICH, A. J., Temporäre Anaerobiose höherer Pflanzen. Landw. Jahrb. 38:51–194. *pls. 1, 2. figs. 2.* 1909.

tuitous alteration in length by turgor changes; but he thinks this explanation precluded by the different behavior of the plants with sugar solutions under aerobic and anaerobic conditions respectively. Because of the great increase in growth late in the culture period, he also rejects the possibility of anaerobic growth being due to residual oxygen, even though there must be some not removable by his methods. Taking everything into consideration, NABOKICH believes that aerobic and anaerobic growth have no necessary connection, being called forth by different factors.

A reading of this paper leaves one unconvinced that the author has established his point, in spite of the apparently prodigious labor the prolonged and very difficult research has involved, with results of minimal consequence. It seems another case of the mountains in labor.—C. R. B.

**Hybridization.**—GIGLIO-TOS[32] publishes an attempt to reach theoretical explanation of the varied phenomena of hybridization. His views are based on his theory of "biomolecular addition" which may be briefly stated. He supposes that a fertilized egg, *A*, consists of a series of molecules *a*, *b*, *c*, *d*, *e*, . . . . , and that after a series of chemical transformations owing to assimilation they arrive finally at a chemical constitution *m*, *n*, *o*, *p*, *q*, . . . . , after which each divides into *2a*, *2b*, *2c*, *2d*, *2e*, . . . . , bringing a return to the original condition. When this occurs, "regeneration of the germ" would be complete. In sexual reproduction if ♂*A* and *B*♀ represent the biomolecules of the two germ cells, the organism developed from the fertilized egg, ♂*AB*♀, might have the capacity of regenerating the whole "biomolecule" which formed it, in which case we would have parthenogenesis; or if complete regeneration is not possible we will have sexual reproduction, each of the germ cells regenerating a part. The case in plants, in which both sexes are usually present in the same individual, is not specifically considered.

From this point of view the writer interprets sexuality, synapsis and reduction, fertilization and hybridization. It is further supposed that the zygote *AB*, while retaining an equal number of male and female biomolecules, yet in the ontogeny undergoes certain modifications, so that the resulting germ cells will be ♂*M* and *N*♀; and that the constitution of these is such that they can be added to each other ("biomolecular addition") to produce again ♂*AB*♀.

On this basis the results of crossing are considered from an a-priori point of view and a number of "laws" are enunciated. Explanations of Mendelian segregation, blending, and other phenomena of hybridization are offered, and predictions made as to the results of cross-breeding reciprocal hybrids. The formal character of the hypothesis makes it probable that it will fail to conform to many of the facts of hybridism, but its viewpoint is very suggestive. For the details of its application see the original paper.—R. R. GATES.

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[32] GIGLIO-TOS, ERMANNO, L'eredità e le leggi razionali dell' ibridismo. Biologica **2**:no. 10. pp. 36. 1908.

**Graft hybrids.**—WINKLER[33] has published a further account of his experiments with graft hybrids of *Solanum nigrum* and *S. lycopersicum*. In all, thirteen graft hybrids have appeared, belonging to five different types, which are named *S. tubingense*, *S. Darwinianum*, *S. Gaertnerianum*, *S. proteus*, and *S. Koelreuterianum*. Of these forms the first three resemble most *S. nigrum*, and the last two resemble the tomato, *S. proteus* being very variable in leaf shape and having leaves similar to *S. Darwinianum*. *S. Gaertnerianum*, like many sexual hybrids, often has sterile anthers. *S. Darwinianum* and *S. Koelreuterianum* are very unlike in their vegetative organs, but similar in their flower characters. *S. proteus* produces reversions to the tomato, which it most resembles, while *S. tubingense* reverts to the nightshade, it nearest parent.

Some viable seeds are produced by the graft hybrids, but the percentage of germination is very small. In *S. tubingense* the length of time required for ripening the fruit is short, like that of the nightshade, while the maturing time for the seeds is intermediate, and hence the ripened fruit contains immature seeds.

The chimeras described in WINKLER's previous papers also recur, and some others are of peculiar character; e. g., one chimera was *S. lycopersicum* on one side and *S. tubingense* on the other, and another was composed of the two graft hybrid forms, *S. tubingense* and *S. proteus*. In *S. nigro-tubingense* one flower had two white petals and three yellow. *S. Darwinianum* similarly originated from a chimera which was partly *S. nigrum* and partly *S. Darwinianum*, and a pure shoot of the latter was obtained only after four decapitations of this branch. *S. Gaertnerianum* appeared five times on different grafts, in some cases as an independent shoot and in others from a chimera.

The forms are all held to be true graft hybrids and not mutations, because they are intermediate between the parents. WINKLER thinks that graft hybrids differ from sexual hybrids in their marked pleiotypy, but it is too early to say what the cause of this may be.—R. R. GATES.

**Heredity in the pea.**—Two papers by DARBISHIRE[34] deal with heredity in the pea. The first is a very interesting analysis of the types of starch grain in round and wrinkled hybrid peas. It is to be hoped that this valuable paper will lead to many other studies of a similar sort, because very little attention has been paid to the ontogenetic development of Mendelian characters. GREGORY[35] had previously shown that round and wrinkled peas possess different types of starch

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[33] WINKLER, HANS, Weitere Mitteilungen über Pfropfbastarde. Zeitschr. Bot. **1**:315–345. *pl. 1. figs. 4.* 1909.

[34] DARBISHIRE, A. D., On the result of crossing round with wrinkled peas, with especial reference to their starch grains. Proc. Roy. Soc. London B **80**:122–135. *figs. 6. tables 8.* 1908.

———, An experimental estimation of the theory of ancestral contributions in heredity. Proc. Roy. Soc. London B **81**:61–79. *tables 8.* 1909.

[35] GREGORY, R. P., The seed characters of *Pisum sativum*. New Phytol. **2**:226–228. 1903.

grains. In the round pea are large potato-shaped grains (*p* grains), while the wrinkled pea has compound grains (*c* grains), averaging six parts to a grain. In addition, both types possess a few very small circular grains and in the wrinkled pea are found occasional *p* grains, though these are very rare. In the hybrid $F_1$ the starch grains are perfectly intermediate between those of the parents, although the character roundness is dominant. The majority of the grains in $F_1$ are large and round; some, however, are compound, averaging three parts to a grain. Heterozygotes (DR) in the $F_2$ were of a similar sort, but extracted wrinkled peas in $F_2$ showed an occasional *p* grain. DARBISHIRE concludes that round differ from wrinkled peas in four pairs of characters: (1) the shape of the pea, (2) its absorptive capacity for water, (3) the shape of the starch grain, and (4) the constitution of the starch grain, i. e., whether single or compound.

In a more recent paper the author tests the theory of ancestral contributions as applied to Mendelian heredity. Yellow and green peas obtained from India, Canada, China, Russia, and other sources gave similar results. The recessive character appearing in $F_2$ was shown to behave as though it was as pure as that borne by a pure race. It was concluded that "there is nothing like ancestral contributions within the limits of a single unit character," and that in such cases in predicting the results of a cross, "the somatic characters not only of the parents and of the ancestors of the individuals mated, but of the individuals themselves, may be left out of account," expectation being based on the theory of the contents of the germ cells.—R. R. GATES.

**Diversity in cotton.**—Several bulletins by COOK and his associates in the Department of Agriculture[36] are not only of great commercial value in directing the activities of cotton growers, but are also of considerable interest as studies in variability and its causes, and the results of crossing. Without attempting to mention all the topics considered, one or two of them may be referred to as of special interest. The diversity found in Egyptian cotton introduced into Arizona is considered to be of four kinds: (1) diversity due to hybridization, (2) diversity due to incomplete acclimatization, (3) diversity due directly to differences in the physical environment, and (4) diversity in different parts of the same plant. Slight differences in the external conditions have large effects in the productivity of individuals by determining the production of sterile or fertile branches.

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[36] COOK, O. F., Reappearance of a primitive character in cotton hybrids. Bureau Pl. Ind., Circ. 18. pp. 11. 1908.

———, The superiority of line breeding over narrow breeding. Bureau Pl. Ind., Bull. 146. pp. 45. 1909.

———, Suppressed and intensified characters in cotton hybrids. Bureau Pl. Ind., Bull. 147. pp. 27. 1909.

COOK, O. F., MCLACHLAN, A., AND MEADE, R. M., A study of diversity in Egyptian cotton. Bureau Pl. Ind., Bull. 156. pp. 60. *pls.* 6. 1909.

COOK. O. F., Local adjustment of cotton varieties. Bureau Pl. Ind., Bull. 159. pp. 75. 1909.

It is found that when a race of cotton is introduced into a new locality it usually shows at once an epidemic of variation in many directions, many of the plants showing a large amount of deterioration. The tendency can be eradicated only by selecting from the best (unmodified) individuals in the new locality. In this manner a reasonab y constant race is finally obtained in the new locality, the process being known as local adjustment. New-place diversity is thus a phenomenon distinct from ordinary fluctuating variability, and of prime importance in connection with acclimatization. These new-place variations are not adaptations to the conditions, but are considered to be "experiments in accommodation" or as "affording the materials from which the more definitely accommodative characters may be developed." Neither are they directly impressed upon the plants by the external conditions, but much of the diversity is believed to represent "transmitted characters which have been able to come back into expression because the change of conditions has disturbed the previous adjustments that selection had established."—R. R. GATES.

**Plants with HCN.**—MIRANDE finds[37] that green plants which contain cyanic compounds, if subjected to the action of chloroform, ether, and other vapors that check photosynthesis, exhale a strong odor of hydrocyanic acid. He proposes therefore to use GUIGNARD'S test[38] in connection with this process to determine what plants contain such compounds. The test requires only a short time and avoids all the complicated and troublesome processes necessary for chemical analysis. Besides it seems to be more delicate and certain. Thus MIRANDE reports that the presence of hydrocyanic acid may readily be detected in *Arum maculatum*, a plant in which the existence of HCN, long in controversy, has lately been demonstrated by analysis.—C. R. B.

**Geotropism and metabolism.**—The only experiments which have claimed to show a direct connection between irritability and metabolism have been those of CZAPEK and BERTEL, who found that in geotropically stimulated roots there was an accumulation of reducing substance, which they identified as homogenistic acid. The precise character of this substance has been controverted. Now come GRAFE and LINSBAUER,[39] who report that in the material used by them (*Lupinus albus* and *Vicia Faba*) the absolute amount of reducing substances (character not determined) is very small and far below the values found by CZAPEK. Moreover, there was no constant difference between the stimulated and the unstimulated roots.—C. R. B.

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[37] MIRANDE, M., Influence exercée par certaines vapeurs sur la cyanogénèse végétale. Procédé rapide pour la recherche des plantes à acide cyanhydrique. Compt. Rend. Acad. Sci. Paris **149**:140–142. 1909.

[38] BOT. GAZETTE **43**:288. 1907.

[39] GRAFE, V., AND LINSBAUER, K., Zur Kenntnis der Stoffwechseländerungen bei geotropischer Reizung. Sitzb. K. Akad. Wiss. Wien Math.-nat. Kl. **118**:907–916. 1909.

# GENERAL INDEX

Classified entries will be found under Contributors and Reviews. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic*.


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